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NOTEWORTHY COLLECTIONS

OREGON

BLEPHARIDACHNE KINGII (S.Watson) Hack. (POACEAE).—Harney Co., vicinity of Fields southwest of Salt Springs and the Borax Lake Area of Critical Environmental Concern along the eastern edge of Guzzler Road. Common halfway up the west side of a butte with *Artemisia spinescens* D.C.Eaton, *Atriplex confertifolia* (Torr. & Frém) S.Watson, *Bromus tectorum* L., and *Eriogonum nidularium* Coville. This population covers an area of roughly 30 m² with 19–28 plants per m², but may extend beyond that. Bunch grasses and appropriate habitat were present outside this 30 m² pocket, but heavy grazing had rendered the plants largely unidentifiable. 42.31704°, -118.54242°, elev. 1300 m, C. Olson 72, 29 June 2017 and 23 September 2017 (WWB22966).

Previous knowledge. *Blepharidachne kingii* is not previously known from Oregon but is widespread across Nevada. This species seems restricted to the Great Basin, with populations also found in California, Idaho, and Utah (Cronquist et al., 1977). *Blepharidachne kingii* is known to occur 150 km south in Humboldt County, NV (ID134329, CPNWH 2019).

Significance. This is the first collection of this species in Oregon. While this collection shows *B. kingii*'s range extends 150 km further north in Oregon than was previously known, it is impossible to know in the absence of other data if this collection is part of a larger historical range that is contracting south towards the Oregon–Nevada border or a recent range expansion from populations in Humboldt County, NV into Oregon.

CLEOMELLA PARVIFLORA A.Gray (CLEOMACEAE).—Harney Co., vicinity of Fields near the Borax Lake Area of Critical Environmental Concern and Salt Springs. Common at the edges of the Salt Springs salt pan with *Nitrophila occidentalis* (Moq.) S.Watson in a 10 m wide band with 40–50 plants per m². 42.30817°, -118.61590°, elev. 1240 m, C. Olson 52, 23 June 2017 (WWB22989).

Previous knowledge. *Cleomella parviflora* has been reported twice in Oregon in the last hundred years—first in 1901 in Harney County, OR in the vicinity of Andrews, OR (exact location not known, but Andrews, OR is roughly 19 km from my collection) by D. Griffiths and E. L. Morris (NY00242420, CPNWH 2019) and a 1997 collection by Florian Wernette in Malheur County, OR, which was later determined to be a misidentified sample of *Cleomella hillmanii* A.Nelson var. *goodrichii* (S.L.Welsh) P.K.Holmgren (CIC26921, CPNWH 2019). Outside Oregon *C. parviflora* is known from moist, alkaline

areas around thermal springs throughout California, Idaho, and Nevada (Vanderpool et al. 2010).

Significance. This is the first collection of *C. parviflora* in Oregon in 116 years, proving *C. parviflora* is a longstanding component of southeastern Oregon's endemic flora that has not been extirpated by a century of grazing, habitat changes, and human disturbance. This collection also confirms that the northern boundary of *C. parviflora*'s range extends further north than was previously known, with the next most northern population of *C. parviflora* occurring 185 km south within the High Rock Canyon Emigrant Trails National Conservation Area of Humboldt County, Nevada (ID134329, CPNWH 2019).

STEPHANOMERIA PAUCIFLORA (Torr.) A.Nelson (ASTERACEAE).—Harney Co., Borax Lake Area of Critical Environmental Concern and the vicinity of Fields. Uncommon throughout the Borax Lake Area of Critical Environmental Concern, and the dune fields along Guzzler Road before Salt Springs Claire Olson 123, 2 June 2018 (WWB23010). Largest population (a few hundred individuals) 42.29852°, -118.62078°, 1240 m with *Aliciella lottiae* (A.G.Day) J.M. Porter, *Artemisia tridentata* Nutt., *Malacothrix torreyi* A.Gray, *Penstemon acuminatus* Douglas ex Lindl. var. *latebracteatus* N.H.Holmgren, *Sarcobatus vermiculatus* (Hook.) Torr., and *Stephanomeria exigua* Nutt.

Previous knowledge. Outside Oregon, *S. pauciflora* is known from Arizona, California, Colorado, Kansas, Nevada, New Mexico, Oklahoma, Texas, Utah, Wyoming, and northwestern Mexico (Cronquist et al. 1997; Gottlieb 2006). *Stephanomeria pauciflora* was collected in 1929 in Malheur County, OR (Collector unknown, SRP000379; CPNWH 2019), and again in 2017 in Harney County by Frank T. Callahan along the Oregon side of the Oregon–Nevada border (SOC25790, CPNWH 2019).

Significance. This collection and my observations verify the presence of *S. pauciflora* within the vicinity of Fields, OR and show the species to be well established within southern Harney County, OR from the Oregon–Nevada border nearly 45 km north to the Borax Lake Area of Critical Environmental Concern.

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DISPERSAL OF SPICEBUSH (*CALYCANTHUS OCCIDENTALIS*, CALYCANTHACEAE)
BY YELLOW JACKETS (GENUS *VESPULA*; HYMENOPTERA: VESPIDAE)

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ABSTRACT

Carnivorous wasps of the family Vespidae are known to seek out and disperse the diaspores of at least two North American and two Asian plant species. Attraction of the wasps to the diaspores is likely due to the release of volatile compounds that signal availability of an elaiosome rich in protein and fat, which the wasps remove before releasing the diaspore. It is thought that this interaction between carnivorous wasps and plants is rare, occurring in just a few plant species. Here, we present our findings on dispersal of spicebush (*Calycanthus occidentalis* Hook. & Arn.) achenes by carnivorous wasps of the genus *Vespula*. Observations and experiments were performed with the goals of discovering: how geographically widespread this interaction is; what the reward system is, if any; and, how wasps detect the achenes. Eight populations of *C. occidentalis* in northern California were used to observe wasps and plants, and to perform experiments on wasp attraction to the achenes. In all examined populations, workers of western yellowjacket (*Vespula pensylvanica* [de Saussure, 1857]) were observed entering mature *Calycanthus* receptacles, removing achenes, taking flight with them, and successfully transporting achenes through the air. Receptacles were found to open upward at an average angle of 45° (SD = 29°), preventing the achenes from falling to the ground when mature. No animals other than wasps were observed visiting the receptacles during the observations. Experiments suggest that wasps are attracted to an elaiosome-like organ of the achene. Nutritional analysis shows that this organ is high in fat and protein. Further experiments using solvent extracts of the achenes suggest that the attraction is likely mediated by volatile compounds.

Key Words: achene, California, fat, protein, reward, vespichochory, volatile.

The vast majority of insect-mediated plant diaspore dispersal is accomplished by ants (Handel and Beattie 1990; Hölldobler and Wilson 1990; Gómez and Espader 1998; Rico-Gray and Oliveira 2007; Lengyel et al. 2009) and is based on well-studied reward systems that usually involve a nutrient-rich accessory organ (elaiosome; Rico-Gray and Oliveira 2007). A less common and under-studied form of plant diaspore dispersal by insects is carried out by flying wasps and bees (Pellmyr 1985; Wallace and Trueman 1995; Jules 1996; Wallace et al. 2009; Zettler et al. 2001; Manohara 2013; Chen et al. 2018). Wasps, particularly those of the genera *Vespa* and *Vespula* (Vespidae) have been found to disperse the diaspores of four plant genera, *Aquilaria* Lam. (Thymelaeaceae; Manohara 2013), *Stemon* Lour. (Stemonaceae; Chen et al. 2018), *Trillium* L. (Melanthiaceae; Jules 1996; Zettler et al. 2001), and *Vancouveria* C. Morren & Decne. (Berberidaceae; Pellmyr 1985). Though the interaction is infrequently observed, its existence in four plant groups from divergent lineages on two continents suggests that it might occur in more groups of plants, and has escaped attention due to the past focus on ants as the major insect dispersers of diaspores.

Here, we report an investigation into wasp-based diaspore dispersal in spicebush, *Calycanthus occidentalis* Hook. & Arn. (Calycanthaceae). Spicebush is a California-endemic shrub and the only member of the Calycanthaceae found in western North America; the other members of the genus are in the southeastern U.S. and China, remnants of a disjunction that dates to the Miocene (Zhou et al. 2006). *Calycanthus occidentalis* is a shrub or small tree, most often found in riparian or other perennially moist microhabitats in the foothills (<1500 m) of the Sierra Nevada, Cascade Range, North Coast Range, and Klamath Mountains.

In the late spring to early summer, spicebush produces large (5–8 cm diameter) flowers, consisting of dark red tepals that open to reveal flattened stamens surrounding the opening of an invaginated, capsule-like receptacle. Individual ovaries are on the walls of this receptacle, and are probably pollinated by small beetles, which access the ovary chamber prior to full opening of the flower by crawling down a shaft produced by the inwardly-bent tips of the tepals (Grant 1950). The receptacle matures into a dry, capsule-like organ containing large (~1 cm long), closely packed achenes, each with a friable, reddish,

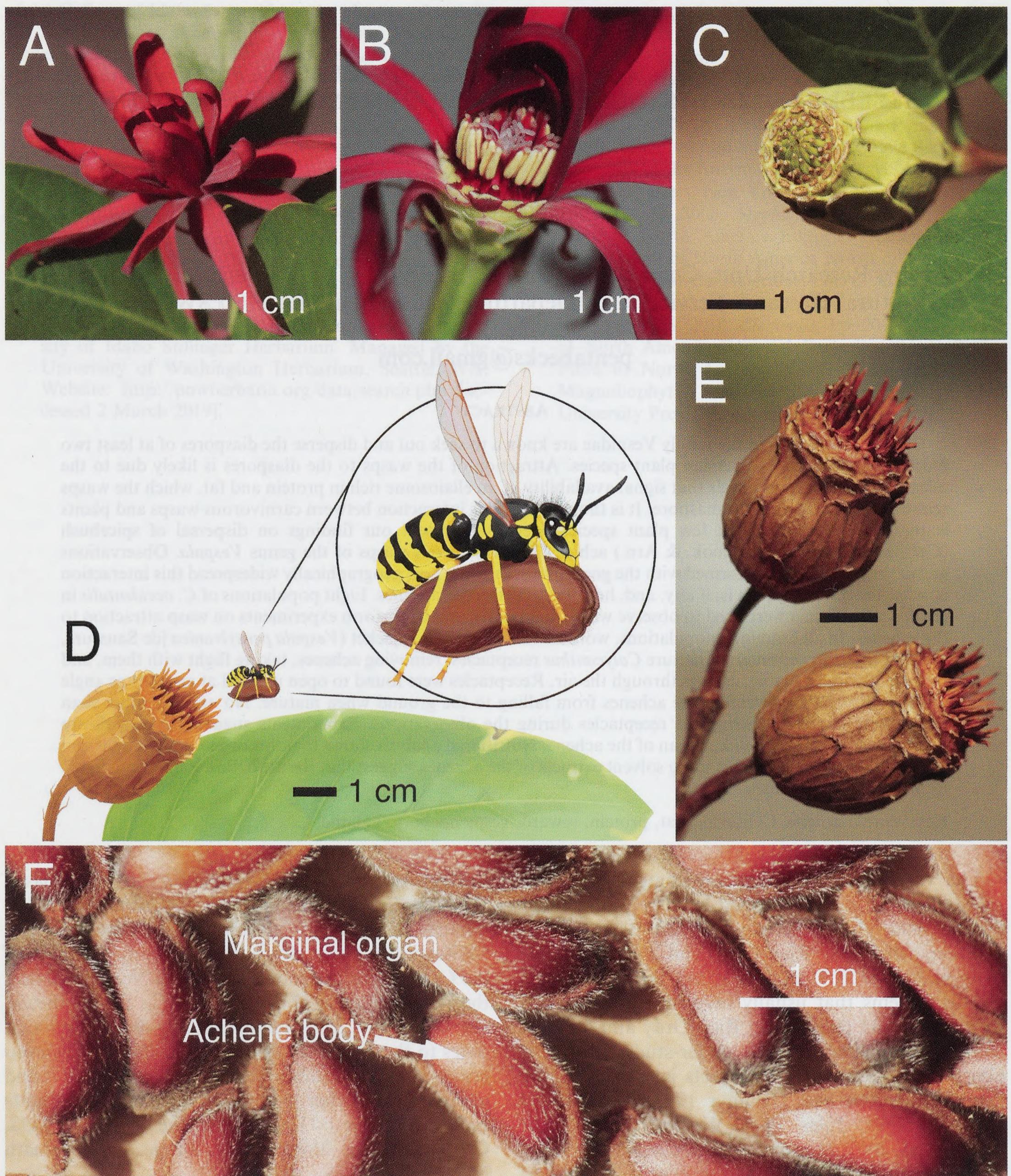


FIG. 1. Focal organisms of the study. (A) flower of spicebush, (B) developing receptacle of spicebush, (C) mature receptacle just prior to opening, (D) drawing of *Vespula pensylvanica* in flight with achene of spicebush (E) dry, open receptacle of spicebush, and (F) detail of achenes, showing the achene body and marginal organ.

annular organ (Fig. 1). Mature receptacles open from the tip, allowing access to the achenes (Fig. 1). Before the present work, nothing was known about dispersal of achenes in *C. occidentalis*.

In August 2016, initial observations were made of wasps (*Vespula pensylvanica* de Saussure, 1857)

visiting achenes placed in a bowl close to an open window at the residence of the first author's mother in the Butte Creek watershed, outside Chico, CA (Vanessa Church, personal communication). Examination of spicebush plants in this area revealed wasps visiting receptacles and removing achenes. As

this interaction between wasps and *C. occidentalis* was not previously reported, an investigation was launched to learn more about the system. Populations of *C. occidentalis* were visited to observe wasp activity, to collect data on receptacle morphology, and to obtain achenes for experiments and analysis of nutritional contents. Experiments were carried out at a subset of the eight focal populations, as well as at sites outside the geographic range of spicebush. The overall aims of this work were to determine: 1) how geographically widespread the interaction may be, 2) what the reward system is, if any, and 3) how wasps detect the achenes.

MATERIALS AND METHODS

In the summer of 2016, eight populations of *C. occidentalis* (Table 1; Fig. 2; Appendix I) were visited by the first author. These populations were selected to represent major population centers of the species (Consortium of California Herbaria 2018). Populations were accessed via vehicle and on foot. At each site, *Vespula* workers and their behavior in and around spicebush receptacles were observed. Observations were carried out for at least 3 hr at each site, and at least ten individual shrubs were examined. The goal of these observations was to assess whether *Vespula* are attracted to *Calycanthus* receptacles in the wild. If a single *Vespula* wasp was observed entering a *Calycanthus* receptacle, this was counted as a successful visitation event; other than confirming that the visitation occurred, no other data was collected; the number of visits was not quantified. At a subset of sites, measurements were taken of the orientation of the mature receptacles, to determine the likelihood that achenes would naturally fall from open receptacles to the ground. Measurements of the receptacle angles were taken using a home-made

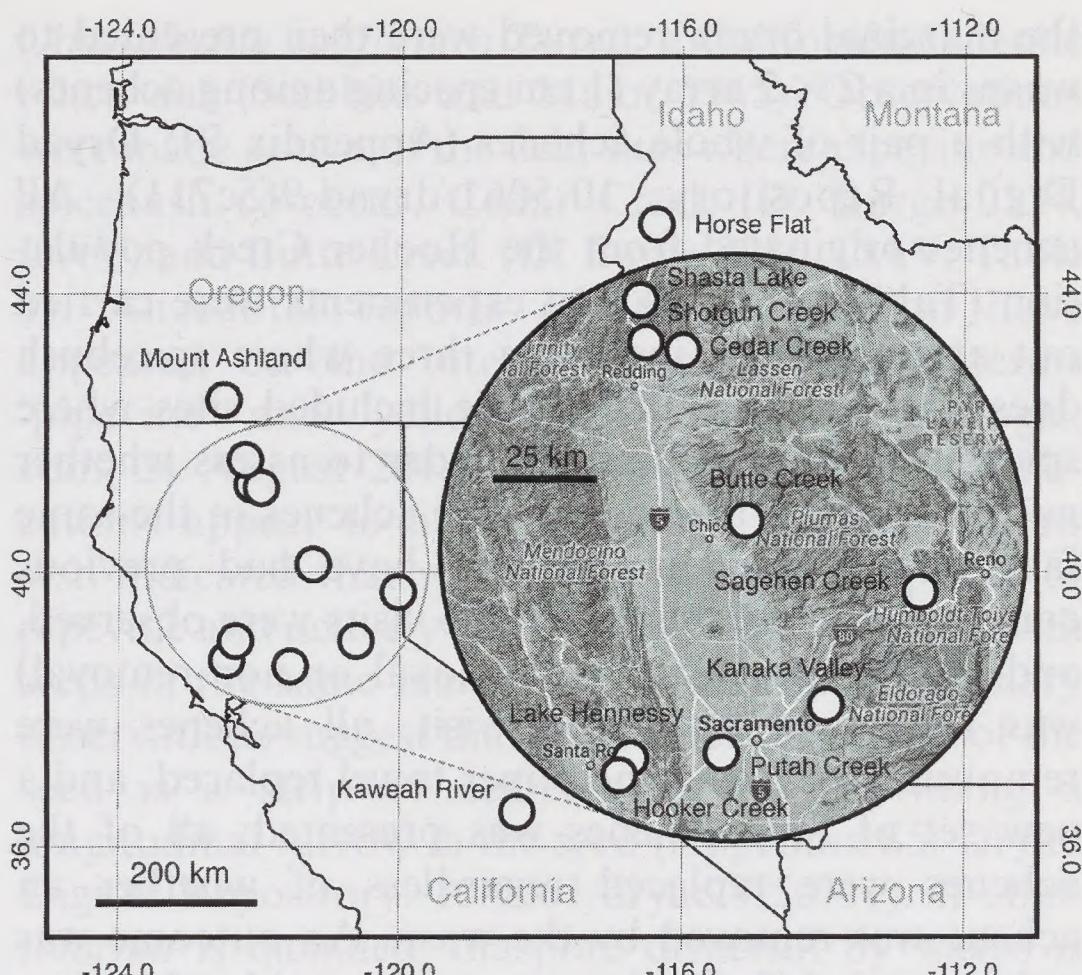


FIG. 2. Map of sites visited for this research.

inclinometer consisting of a protractor with a level and a plumb-bob attached. The angle was measured along the longitudinal axis of the receptacle, and recorded as the difference from horizontal (0°), with a maximum of 90° in either direction (i.e., a range from -90° to 90°). At a subset of the sites, achenes were collected from open receptacles and allowed to dry in open paper bags for 12 hr before they were stored for later use in the same paper bags.

A series of experiments were carried out to determine: 1) whether wasps are attracted to the marginal organ or to the remaining part of the achene; 2) whether achenes are returned to the nest after collection by wasps; and 3) whether attraction to achenes is visual or olfactory. In the first experiment, the marginal organ was removed from a set of achenes using a razor. A pair of achenes with

TABLE 1. SITES VISITED FOR ACHENE COLLECTING, MEASUREMENTS, AND EXPERIMENTAL WORK. Plant voucher = collection code for spicebush voucher, and reference code for site; all voucher specimens were deposited at DAV (Appendix I). Wasp voucher = study-specific collection code for wasp voucher specimens; all specimens deposited at the U. S. Davis Bohart Museum of Entomology (Appendix II). Angle = sites at which the angles of the receptacle openings were measured. Mass = sites where achene mass was measured. Under Experiments, Choice indicates sites where achene choice experiments were carried out; Nest indicates sites where achenes were presented to nests and nests then excavated to determine if achenes were returned to the nest; Extract indicates source populations for achene extracts used in trapping experiments.

Site name	Plant voucher	Wasp voucher	Angle	Mass	Experiments		
					Choice	Nest	Extract
Butte Creek	D. Burge 2122	1000	x	x	x		x
Hooker Creek	D. Burge 2123	1005, 1006	x	x	x		
Sagehen Creek		1007, 1008			x	x	
Shasta Lake	D. Burge 2125	1010	x	x	x		
Shotgun Creek	D. Burge 2127	1011	x	x	x		
Mount Ashland		1012, 1013			x		
Cedar Creek	D. Burge 2132	1017	x		x		
Horse Flat		1019, 1020			x		
Putah Creek		1022				x	
Kanaka Valley		1023				x	
Kaweah River	D. Burge 2201						x
Lake Hennessy	D. Burge 2284						x

the marginal organ removed were then presented to wasps in a 2×2 array (1 cm spacing among achenes) with a pair of whole achenes (Appendix S1; Dryad Digital Repository: 10.5061/dryad.9f5c711). All achenes originated from the Hooker Creek population (Table 1; Fig. 2), but experiments were carried out at eight sites, including three where spicebush does not occur (Table 1). We included sites where spicebush does not occur in order to assess whether naïve wasps are attracted to the achenes in the same fashion as wasps that might have had previous contact with *Calycanthus*. Wasp visits were observed, and the outcome (achene removal or non-removal) was recorded. After each visit, all achenes were removed, the underlying paper towel replaced, and a new set of four achenes was presented; all of the achenes were replaced regardless of whether an achene was removed by the wasp. An outcome was only recorded if an achene was removed by the wasp from the experimental arena. Experiments were carried out for 2 hr at each site, between 1500–1800 hr (Table 1). To statistically test achene preference, we conducted a two-sided binomial test in R (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). The binomial test explicitly treated each of the wasp visits as having only two possible outcomes: 1) achene removed or 2) achene not removed. The third possible outcome of a wasp visit, ‘no choice,’ was therefore treated as a nuisance parameter and not modeled. Finally, voucher specimens for each wasp species visiting the achenes were obtained at each site and deposited at the Bohart Museum of Entomology (Table 1; Appendix II).

In the second experiment, three sites were selected (Table 1). At each site, 100 intact achenes were presented in an open dish within 10 m of a single *V. pensylvanica* nest. After all the achenes were taken by wasps, the nest was subdued using carbon dioxide gas, and excavated. The number of achenes found in the nest, where they were located, and their condition, was recorded. Voucher wasp specimens were obtained from each nest and deposited at the Bohart Museum of Entomology (Table 1; Appendix II).

In the third experiment, an organic solvent was used to extract whole achenes, and the resulting extract was tested for its ability to attract wasps. We tested achenes from three sites (Table 1). For each of the three sites, 100 intact achenes were soaked in 100 mL analytical grade pentane for 12 hr. The extract was evaporated on a Whatman 1001-125 Qualitative Filter Paper Circle, and the filter paper placed in a RESCUE! Non-Toxic Yellowjacket Trap (Sterling International, Inc., Spokane, WA). A negative control, a filter paper circle from which 100 mL of pure pentane was evaporated, was used for comparison. The four traps (one for each site extract, plus control) were suspended 1 m apart on a rope tied between two trees. The traps were left for a 5 hr period in the afternoon (1300–1800 hr), then the

number of trapped wasps was counted. The experiment was repeated three times on three different days (21–23 August 2017), using a new overnight extraction on each occasion. All experiments were performed at the Butte Creek site (Table 1).

Because preliminary evidence suggested that the marginal organ of the achene was the part most attractive to wasps, nutritional analysis of this organ was carried out at the Michigan State University Diagnostic Center for Population and Animal Health. Variables measured included proportion of crude protein, crude fat, water-soluble carbohydrates, simple sugars, and starch (all on a dry mass basis). A total of 2 g of the achene marginal organ (Fig. 1) from the Hooker Creek population (Table 1; Fig. 2) was sent for analysis.

RESULTS

At all but two of the sites visited for observations (Table 1), workers of *V. pensylvanica* were seen hovering near the openings of mature receptacles, entering the receptacles, exiting the receptacles with achenes, and flying away with the achenes (see Appendix S2 for a video of interaction; Dryad Digital Repository: 10.5061/dryad.9f5c711). In most cases, wasps flew out of sight immediately, but a few landed on nearby vegetation and dropped the achene to the ground. Another vespid wasp, *Dolichovespula maculata* (Linnaeus, 1763) was also observed hovering near the openings of spicebush receptacles at the Shasta Lake site, but did not enter the receptacles.

Across all five populations (Table 1), the average orientation of the receptacles was 45° ($SD = 29^\circ$, $n = 484$, Appendix S3, Dryad Digital Repository: 10.5061/dryad.9f5c711).

In the first experiment, in which wasps were allowed to choose between whole achenes and achenes with the marginal organ removed (Table 1, ‘Choice’), between 18 and 101 trials were conducted at each of the eight field sites (Table 1; Fig. 2). At every field site, whole achenes were preferred over achenes with the marginal organ removed ($P < 0.001$; one-sided binomial tests, $H_A = \text{‘greater’}$).

In the second experiment, in which achenes were taken by wasps to the nest (Table 1, ‘Nest’), only a few achenes were recovered from the excavated nests at each site (Sagehen Creek: $n = 5$; Putah Creek: $n = 10$; Kanaka Valley: $n = 1$). In all cases, the provided supply of achenes was located by the wasps within 5 min, and depleted by the time the author returned 5 hr later. In most cases, a wasp took flight with an achene and flew out of sight, suggesting that most wasps were visiting from nests other than the one under direct observation. At all sites, at least one wasp was observed entering the focal nest with an achene, but the nests were not observed continuously throughout the 5 hr time interval, so data were not collected on the fate of each seed taken by a wasp. In all cases, recovered achenes were found at the bottom of the nest (the likely refuse area of the nest

[MacDonald et al. 1975]), and were stripped of their marginal organ (Appendix S4; Dryad Digital Repository: 10.5061/dryad.9f5c711).

In the third experiment, in which wasps were trapped using an extract of the whole achenes, no wasps were trapped in the control traps, while between 11 and 46 wasps were recovered in the traps baited with extract (Butte Creek: 46 wasps; Kaweah River: 21 wasps; Lake Hennessy: 11 wasps; Table 1).

Nutritional analysis revealed that the achene marginal organs from Hooker Creek comprised 21.6% crude protein, 5.9% crude fat, 1.8% water-soluble carbohydrates, 0.5% simple sugars, and 0.3% starch. All of these measurements are on a dry mass basis.

DISCUSSION

Our work provides preliminary evidence that wasps of the genus *Vespa* act as dispersers of *C. occidentalis*. Our survey of wild *C. occidentalis* stands has shown that visitation of *C. occidentalis* receptacles by *Vespa* is a common interaction in the wild (Table 1). Our follow-up choice experiment provided evidence that the marginal organ of the achene is the part of the diaspore attractive to wasps, while nutritional analysis of this organ showed that fat and protein is the likely reward provided by the plant to its dispersers. The fat and protein content of the marginal organ, comparable to that of lean chicken, pork, or beef (Kerth 2013), is consistent with the typical food sources of *Vespa* wasps (Akre et al. 1981), voracious predators and/or scavengers well known for their attraction to high-protein food sources. Compared to other food bodies provided by plants as a reward for insect dispersers (primarily ants), the marginal organ of *C. occidentalis* ranks amongst the highest yet recorded in terms of fat and protein contents (Fischer et al. 2008). Finally, our experiments on volatile extract of the achenes (Table 1), while preliminary, indicate that olfaction plays a critical role in the *Vespa*-*Calycanthus* interaction, likely signaling the presence of the fat and protein reward.

Additional work is clearly needed in order to characterize and test this interaction in more detail, particularly research into other potential dispersers of the achenes (e.g., ants and rodents) and the details of the reward and detection system. Research into the latter subject (Beck et al. 2019) suggests that detection of spicebush achenes by *Vespa* wasps is based on a volatile chemical signature considerably different from the chemical signature recently elucidated in Chinese *Stemona* (Chen et al. 2018), a plant with seeds dispersed by wasps of the Eurasian genus *Vespa*, a close relative of *Vespa*. Interestingly, the complex chemical signature of spicebush achenes included volatiles identified as chemical cues from several other *Vespa* food sources (Beck et al. 2019).

In the course of this research, it was also observed that *V. pensylvanica* visits capsules of pipevine

(*Aristolochia californica* Torr.), a California-endemic relict vine (Stebbins and Major 1965). Observations were made at two of the field sites where pipevine and spicebush co-occur, Cedar Creek (D. Burge 2134, DAV) and Butte Creek (D. Burge 2286, DAV; Table 1). Anecdotal reports of this interaction have appeared on the internet (search of the terms 'pipevine' and 'yellowjacket,' <http://www.google.com>, 21 August 2018), but no peer-reviewed publications appear to have mentioned it. Observations also indicated that wasps visit dehiscing capsules of pipevine and actively remove seeds, taking flight with seeds in the same manner as spicebush. Preliminary observations suggest that the attractive portion of the seed is a strip of soft, spongy tissue filling a longitudinal furrow in the seed (Appendix S5; Dryad Digital Repository: 10.5061/dryad.9f5c711). If *Aristolochia* is included, diaspore dispersal by wasps is now known to occur in five genera, each from a different order (*Aquilaria*, Malvales; *Aristolochia*, Piperales; *Calycanthus*, Laurales; *Stemona*, Pandanales; *Trillium*, Liliales; *Vancouveria*, Ranunculales).

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APPENDIX I

CALYCANTHUS POPULATIONS INCLUDED IN THIS STUDY

For each population, the format is as follows: collector name and number, name of locality, county, GPS coordinates (WGS84 Datum), County, State. Vouchers deposited at the U. C. Davis Center for Plant Diversity (DAV).

Calycanthus occidentalis.—D. Burge 2122, 6 Aug 2016, Butte Creek (GPS: 39.7930, -121.6625), Butte County, CA. D. Burge 2123, 20 Aug 2016, Hooker Creek (GPS: 38.3620, -122.4684), Sonoma County, CA. D. Burge 2125, 25 Aug 2016, Holiday Harbor (GPS: 40.8042, -122.3121), Shasta County, CA. D. Burge 2127, 26 Aug 2016, Shotgun Creek (GPS: 41.0538, -122.3826), Shasta County, CA. D. Burge 2132, 31 Aug 2016, Cedar Creek (GPS: 40.7782, -122.0047), Shasta County, CA. D. Burge 2201, 20 Nov 2016, South Fork Kaweah River (GPS: 36.3961, -118.8810), Tulare County, CA.

APPENDIX II

VEСПULA POPULATIONS INCLUDED IN THIS STUDY

For each population (Table 1), the format is as follows: collector name and number, description of locality, county, GPS coordinates, County, State. All voucher specimens deposited at the Bohart Museum of Entomology, U. C. Davis. All collections are workers.

Vespula acadica.—D. Burge 1008, 22 Aug 2016, Sagehen Creek (GPS: 39.434, -120.2588), Nevada County, CA.

Vespula alascensis.—D. Burge 1006, 21 Aug 2016, Hooker Creek (GPS: 38.362, -122.4684), Sonoma County, CA. D. Burge 1013, 27 Aug 2016, Mount Ashland (GPS: 42.0749, -122.7151), Jackson County, OR. D. Burge 1020, 3 Sep 2016, Horse Flat (GPS: 44.7753, -116.5414), Adams County, ID.

Vespula pensylvanica.—D. Burge 1000, 15 Aug 2016, Butte Creek (GPS: 39.793, -121.6625), Butte County, CA. D. Burge 1005, 21 Aug 2016, Hooker Creek (GPS: 38.362, -122.4684), Sonoma County, CA. D. Burge 1007, 22 Aug 2016, Sagehen Creek (GPS: 39.434, -120.2588), Nevada County, CA. D. Burge 1010, 25 Aug 2016, Shasta Lake (GPS: 40.8043, -122.3121), Shasta County, CA. D. Burge 1011, 26 Aug 2016, Shotgun Creek (GPS: 41.0538, -122.3826), Shasta County, CA. D. Burge 1012, 27 Aug 2016, Mount Ashland (GPS: 42.0749, -122.7151), Jackson County, OR. D. Burge 1017, 31 Aug 2016, Cedar Creek (GPS: 40.7783, -122.0048), Shasta County, CA. D. Burge 1019, 3 Sep 2016, Horse Flat (GPS: 44.7753, -116.5414), Adams County, ID. D. Burge 1022, 13 Oct 2016, Putah Creek (GPS: 38.5293, -121.761), Yolo County, CA. D. Burge 1023, 20 Oct 2016, Kanaka Valley (GPS: 38.7534, -121.026), El Dorado County, CA.

ECOLOGICAL CHARACTERISTICS AND DISTRIBUTION OF *ARBUTUS XALAPENSIS* (TEXAS MADRONE) POPULATIONS IN CENTRAL TEXAS

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ABSTRACT

Arbutus xalapensis Kunth (Texas madrone, Ericaceae) is found in western and central Texas, but its ecological characteristics are little known. Mature *A. xalapensis* plants were found in the Albert and Bessie Kronkosky State Natural Area in Kendall and Bandera counties, central Texas (29.740278 N, -98.838333 W). Habitats studied included *Acer grandidentatum* Nutt. (bigtooth maple) canyon bottoms, *Juniperus ashei* J. Buchholz/*Quercus* L. sp. (Ashe juniper/mixed oak) hillsides, and *J. ashei* uplands. Population characteristics were compared to habitat and surface geology. A total of 98 *A. xalapensis* plants were found in the communities studied. Differences were found for all parameters except height. Upland *A. xalapensis* trees had the lowest mean (\pm SD) density (2 ± 3 plants/ha), highest basal area (210 ± 190 cm^2/plant), community elevation (573 ± 14 m) and height (4.09 ± 1.70 m/plant). Hillside communities had the highest density (61 ± 38 plants/ha), but lower basal area (110 ± 170 cm^2/plant). The canyon bottom plant basal area was 80 ± 100 cm^2/plant and density was 10 ± 5 plants/ha. The canyon bottoms had the deepest soil (27.2 ± 20.4 cm) and lowest elevation (510 ± 16 m). When geological substrates were examined, 128 additional plants were found. The largest plants were on the Fort Terrell member of the Edwards limestone (hard limestone, 230 ± 220 cm^2/plant), but density was the lowest (2 ± 3 plants/ha). Whereas greater density was on the Upper Glen Rose limestone (softer limestone, 16 ± 7 plants/ha), where plants were smaller (110 ± 150 cm^2/plant). Community type and geological substrate seem critical for growth of this species.

Key Words: basal area, Edwards's limestone, Glen Rose Limestone, habitat preference, *Juniperus* woodland, juniper/oak woodland, limestone soil, plant density.

Species establish in particular habitats based on the biotic and abiotic characteristics of the habitat and the specific needs or requirements of the species (Morin 2011; Keddy 2017). Showing the exact location where a specific plant, species, or community occurs is relatively easy to do, but determining the niche and requirements for an individual species is very difficult (Keddy 2017). Understanding community necessities is even more difficult due to the large number of species and the multitude of requirements. Studying a single species within a larger community can help one understand how the whole community functions (Joshi and Joshi 2009; Keddy 2017).

Arbutus xalapensis Kunth (Texas madrone, Ericaceae) appears to have a disjunct distribution in Texas, found on the Balcones Escarpment in the southeastern and south-central Edwards Plateau and in the mountains of the Trans – Pecos region of west Texas (Fig. 1). In earlier quantitative plant ecological studies in central Texas *Arbutus xalapensis* was not detected in transects where plant communities were measured (Van Auken et al. 2017). However, it was sighted in the area in a number of places (Van Auken, personal observation). Its density was so low it was not found in any of the quadrats sampled or in any of the communities surveyed. Based on the size of the sample, at least one-half hectare would have to be completely examined before *A. xalapensis* would be encountered. This species is not listed as an

endangered or threatened species (Poole et al. 2007), but it is fairly rare in central Texas. There seem to be some specific conditions required for the presence and growth of this species, but at this point, they are not known.

Estimating abundance or density and other aspects of a rare or elusive species is difficult to do (Thompson 2004). These are species that have low density, a restricted distribution, or a low probability of detection. Usually, a rare plant study will define a geographic area containing the species of interest to study and then partition the area into sampling units, such as communities or habitats, then subsequently divide it into plots, transects, and /or quadrats (Thompson 2004). Thus, the procedure seems to be a two-step process requiring a two stage sampling design. Therefore, the selection of sampling units or habitats is the first stage and the counting or measuring of individuals is the second stage (Thompson 2004).

Arbutus xalapensis is found in western as well as central Texas, but its ecological characteristics are not well known. It is one of at least 12 species of *Arbutus* worldwide (Gonzalez-Elizondo et al. 2012; USDA 2016). It is an evergreen tree, typically 4–6 m tall, but can be up to 15 m tall (Sorensen 1995; Mackay 1996) with a trunk circumference up to 2.5 m under favorable conditions (Tirmenstein 1990, Fig. 2). In the United States, *A. xalapensis* occurs in Texas and New Mexico, but its distribution continues

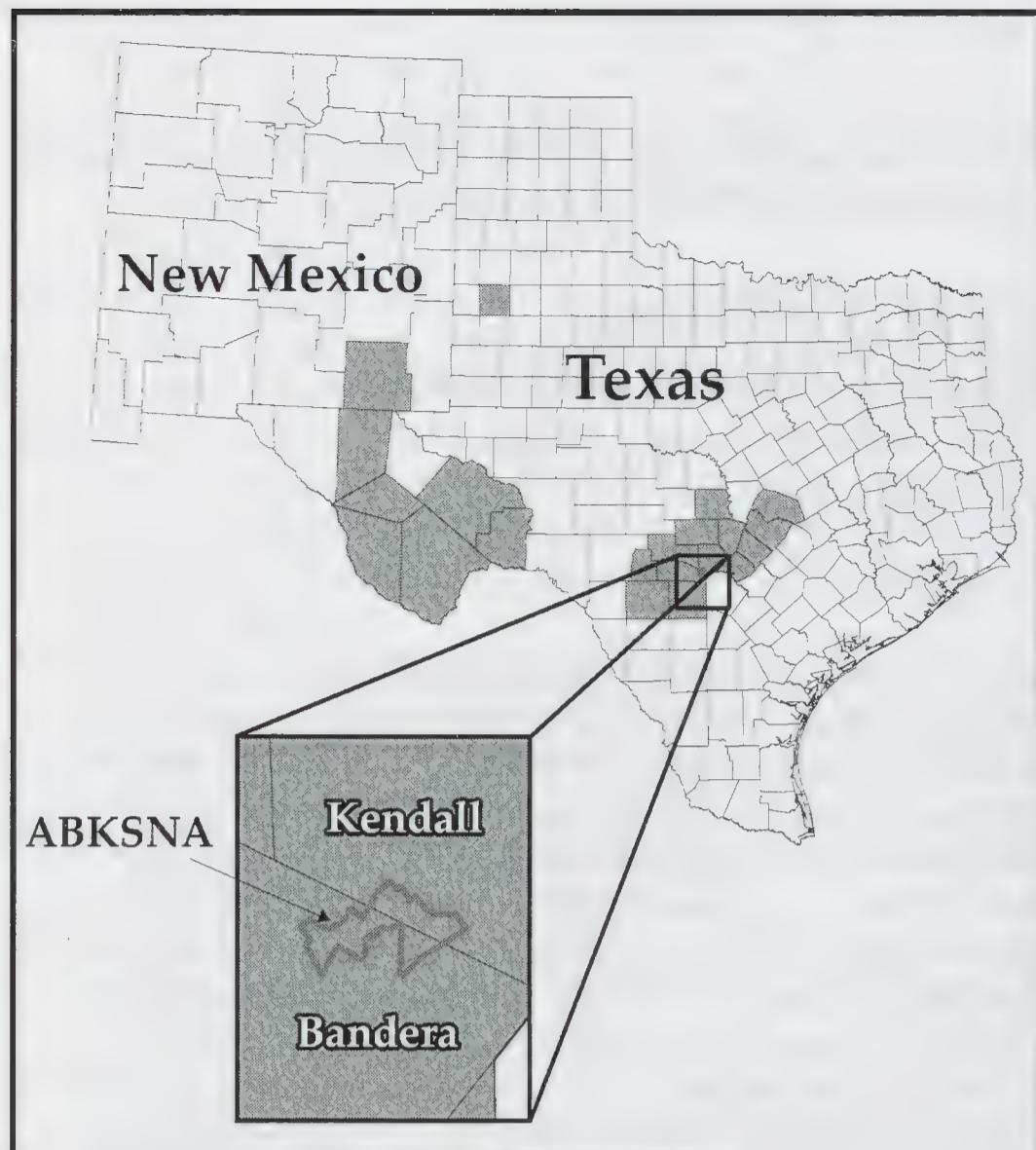


FIG. 1. Map of New Mexico and Texas showing county outlines and shaded counties having *Arbutus xalapensis* plants. The blowup shows most of Kendall and Bandera counties with the outline and arrow showing the Albert and Bessie Kronkosky State Natural Area where the study was carried out (approximately 29.740278 N, -98.838333 W).

southward at higher elevations through most of Mexico, as well as in Guatemala, Honduras, El Salvador, and Nicaragua (Sorensen 1995). In southern Mexico, its elevation ranges from 1500–3400 m in forests with canopy heights of 25–33 m (Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). *Arbutus xalapensis* is found on the Balcones Escarpment in the southeastern and south-central Edwards Plateau and in the mountains of the Trans-Pecos region of west Texas at elevations of about 1219–2286 m (Tirmenstein 1990). This elevation suggests plants are above the Chihuahuan desert communities, probably on hillsides above the desert.

Arbutus xalapensis is reported growing in wooded canyons, western slopes, and dry creek beds (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). It is reported in riparian woodlands with *Populus deltoides* W. Bartram ex Marshall (Eastern cottonwood), *Salix exigua* Nutt. (coyote willow), *Quercus grisea* Liebm. (gray oak), and *Acer grandidentatum* Nutt. (bigtooth maple) (Tirmenstein 1990). Thus, *Arbutus xalapensis* has been documented in a variety of communities containing multiple species of *Quercus* L. (oak), *Juniperus* L. (juniper), *Pinus* L. (pine), and *Ulmus crassifolia* Nutt. (cedar elm) (Tirmenstein 1990). Consequently, its specific habitat seems uncertain and habitat requirements are not known. Much of what is reported for *A. xalapensis* seems to consist of anecdotal or general observations.

In the Edwards Plateau region of Texas, *J. ashei* has been reported to serve as a nurse tree for juvenile *A. xalapensis* plants (Tirmenstein 1990), and juveniles are rarely present beneath mature *A. xalapensis* trees (Van Auken personal observation; also described in Whitenberg and Hardesty 1978). *Juniperus* mulch may increase the soil water-holding capacity, allowing more successful *A. xalapensis* establishment and/or *J. ashei* trees or thickets may protect the juveniles from herbivory (Tirmenstein 1990; Van Auken, personal observation). Light intensity and water availability have been shown to have significant impacts on seedling development (Whitenberg and Hardesty 1978). Seedlings of some other species can germinate in shade and then grow slowly for more than 35 years, but seem to require full sun to mature (Van Auken et al. 2004; Kane et al. 2011). The same may be true for *A. xalapensis* plants, but this is unknown at present.

The purpose of this study was to examine some of the ecological characteristics of populations of *Arbutus xalapensis* in central Texas. This project seeks to identify various biotic and abiotic factors that may influence the growth and distribution of *A. xalapensis* populations across the landscape in the Edwards Plateau region of Texas.

METHODS

Study Site

This study was carried out within the southeastern portion of the Edwards Plateau ecological region of Texas (approximately 29.740278 N, -98.838333 W), referred to as the Balcones Canyonlands (Fig.1). The Balcones Canyonlands are characterized by dry to mesic slopes supporting *Juniperus ashei* - *Quercus fusiformis* Small (live oak) - *Diospyros texana* Scheele (Texas persimmon) woodlands and *Taxodium distichum* Kunth. (bald cypress) - *Carya illinoiensis* (Wagninh.) K.Koch (pecan) - *Celtis laevigata* (Kunth.) Spreng. (hackberry) - *D. texana* riparian communities (Riskind and Diamond 1988). The study site is located within the eastern portion of the Edwards Plateau, which has a mean annual precipitation of about 85 cm/yr, with considerable variation and almost no rainfall in June, July, and August (Riskind and Diamond 1988; Van Auken and Ford 2017). In addition, steep walled canyons and some north facing slopes support limited deciduous communities (Van Auken 2018). The east-central Edwards Plateau average summer high temperature is 35°C and the average winter low temperature is 4°C (Riskind and Diamond 1988).

The specific research study site is located within the Albert and Bessie Kronkosky State Natural Area (ABKSNA) within portions of both Bandera and Kendall counties, TX, and is approximately 1520 hectares (3757 acres), and is high-fenced (Fig.1). The study area ranges in elevation from approximately

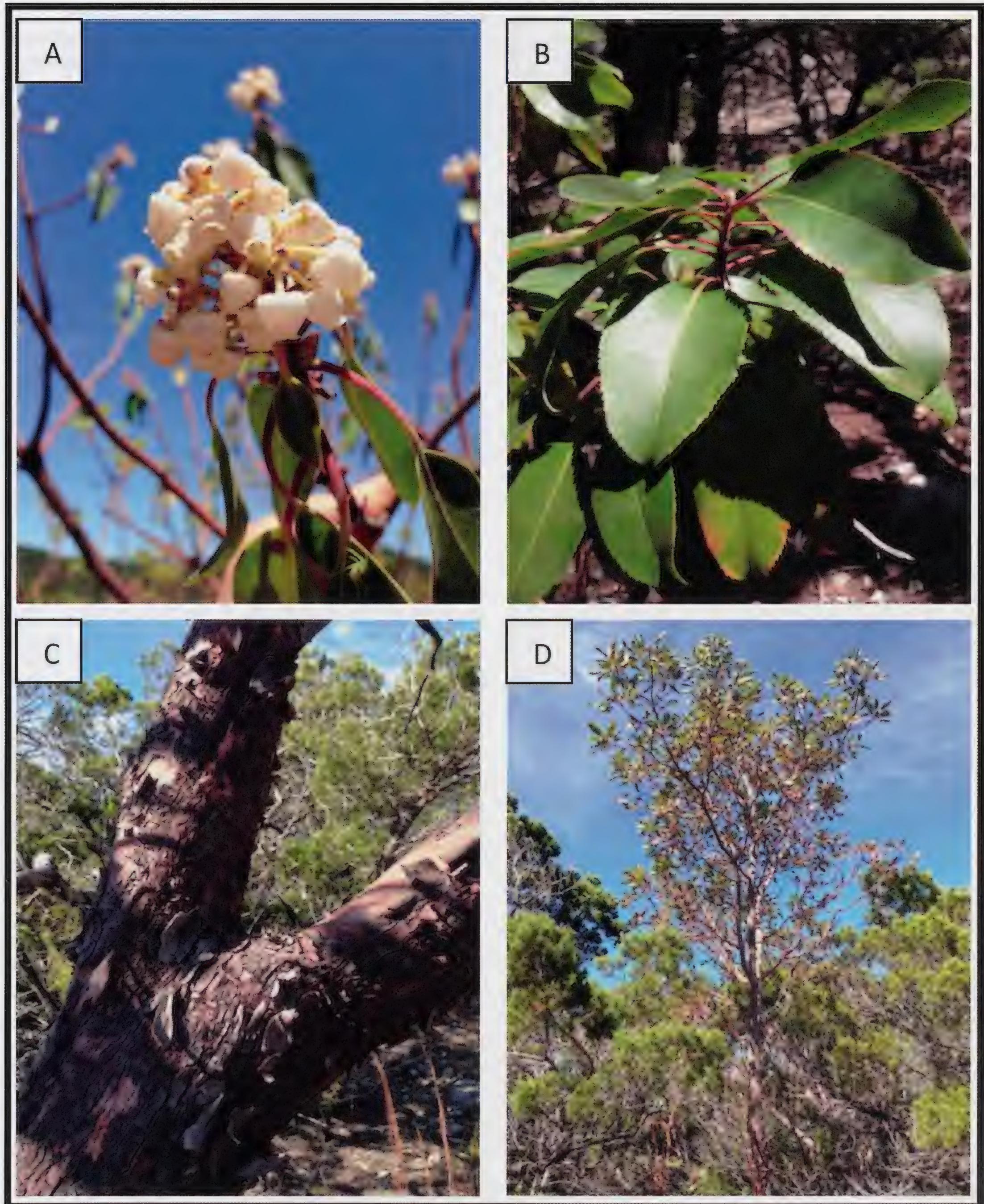


FIG. 2. General pictures of *Arbutus xalapensis* taken at the study site showing notable traits. (A) *Arbutus xalapensis* inflorescence, (B) *A. xalapensis* leaves, (C) *A. xalapensis* bark exfoliation, and (D) mature *A. xalapensis* tree at the Albert and Bessie Kronkosky State Natural Area.

481–614 m above mean sea level (Van Auken et al. 2017). Geologic formations present at the site include the Fort Terrett Member of the Edwards Limestone formation in the upper elevations and Upper Glen Rose limestone formation below the Edwards with

relatively deep calcareous silty clay soil (Mollisols over limestone bedrock, USDA NRCS 2016). In the canyon bottoms at lower elevations the soils are deeper and mostly overlay Upper Glen Rose limestone (USGS - TWDB 1976).

Sampling Methods

Vegetation surveys were carried out in the “Tin Cup Canyon” and associated areas in the north-eastern portions of the ABKSNA (Van Auken et al. 2017). Despite their close proximity (< 0.25 km), the upland and canyon communities differ in many respects. The upland communities were relatively flat with shallow soils, while the canyon communities had greater slopes and deeper soils. Van Auken et al. (2017) found less dense canopy cover within the upland juniper canopies than beneath maple canopies in canyons, however, the understory in the uplands were more densely vegetated than canyon understory communities. Dominant canyon species were found to be *Acer grandidentatum*, *J. ashei*, *Prunus serotina* Poit. and Turpin, and *Quercus laceyi* Small. While the dominant upland species were *J. ashei* and *Sophora secundiflora* (Ortega) Lag. ex DC. However, no *A. xalapensis* juveniles or trees were reported (Van Auken et al. 2017).

Three distinct habitats were chosen for this study: canyons bottoms, hillsides, and uplands. Each habitat was surveyed specifically for *A. xalapensis*. Surveys consisted of arbitrarily walking through the various habitats until an *A. xalapensis* individual was found and then measuring basal diameter (cm), height (m), and soil depth (cm), as well as collecting GPS coordinates and elevation, then resuming the search for additional *A. xalapensis* plants. This process was replicated in each habitat type in the Tin Cup Canyon area. To account for non-uniformity in basal diameter, 80 cm tree calipers were used to measure basal diameter at a minimum of two points per tree. These measurements were taken at ground level and then averaged (Van Auken et al. 1981; Bush and Van Auken 2015). Height was measured using a marked pole (Powell 2005; Bush and Van Auken 2015). Between two and four soil depth measurements, on opposite sides of *A. xalapensis* trees were made by hammering 60 cm long rebar into soil until reaching bedrock (Larcher 2003). After reaching the bedrock, the rebar was removed and soil penetration (depth) was measured on the rebar using a measuring tape (Van Auken et al. 1981).

Due to low density, *A. xalapensis* plants were difficult to locate. Previous uses of the quadrat procedure did not include any *A. xalapensis* individuals in an earlier study despite density stabilization curves indicating adequate sampling (Van Auken et al. 2017). Thus, a distance technique was used to sample these populations (Cottam and Curtis 1956). The nearest neighbor method was used, but only *A. xalapensis* individuals were measured (Cottam and Curtis 1956; Barbour et al. 1987). Mature trees were included if their basal diameters were greater than 1 cm and were greater than 1.56 m in height (Bush and Van Auken 2015). Coordinates of each mature *A. xalapensis* tree

located were uploaded into ArcMap (Version 10.3, ESRI, Inc., Redlands, CA) and distances between mature *A. xalapensis* trees were later determined. The nearest neighbor was restricted to the nearest mature *A. xalapensis* tree found within an 180° area of inclusion from the base of the first tree found and at a perpendicular to the direction of travel (Cottam and Curtis 1956; Barbour et al. 1987). The distance from one individual *A. xalapensis* tree to its nearest neighbor of the same species was found using GPS coordinates (Cottam and Curtis 1956; Barbour et al. 1987; Kane and Ryan 1998). GPS coordinates were also used to measure elevation above mean sea level. The mean distance between neighbors across all plants encountered in each community was determined and *A. xalapensis* density was calculated as follows: total density = $10,000\text{m}^2 / (2 * \text{mean distance}^2)$ (Barbour et al. 1987). Density stabilization curves showed stable density or sampling adequacy in all habitats examined (Davis and Van Auken, unpublished data).

Geologic Survey

To determine the importance of the underlying geology to the density of *A. xalapensis*, data from another area were collected and analyzed using a geologic map in ArcMap (USGS - TWDB 2007). All data collection techniques were consistent with those previously described. Transects were carried out on the Fort Terrett Member of the Edwards limestone and Upper Glen Rose Formation. Measurements included density, basal area, height, and soil depth. Sample size was 128 *A. xalapensis* plants.

Statistical Analysis

To show differences among habitat types, JMP statistical software was used (Version 12, SAS Institute, Cary, NC; Sall et al. 2012). Initially, data were organized by habitat groupings (canyon, hillside, and upland), and then analyzed. Summary statistics (means and standard deviations) were calculated for each habitat type and each data set was tested for normality using the Shapiro-Wilk test. Shapiro-Wilk tests resulted in non-normally distributed data. Due to differences in sample sizes and high variance, as well as non-normally distributed data, non-parametric statistics were utilized. Kruskal-Wallis tests were completed to determine if the density, height, elevation, basal area, and soil depth parameters were different between habitat types ($\alpha = 0.05$) (Sall et al. 2012). Dunn's post hoc test was used to show where significant differences occurred (Dinno 2015). The non-parametric Mann-Whitney U tests were used to show significant differences in the parameters listed above between communities on Fort Terrett and Glen Rose geological substrates ($\alpha = 0.05$) (Sall et al. 2012).

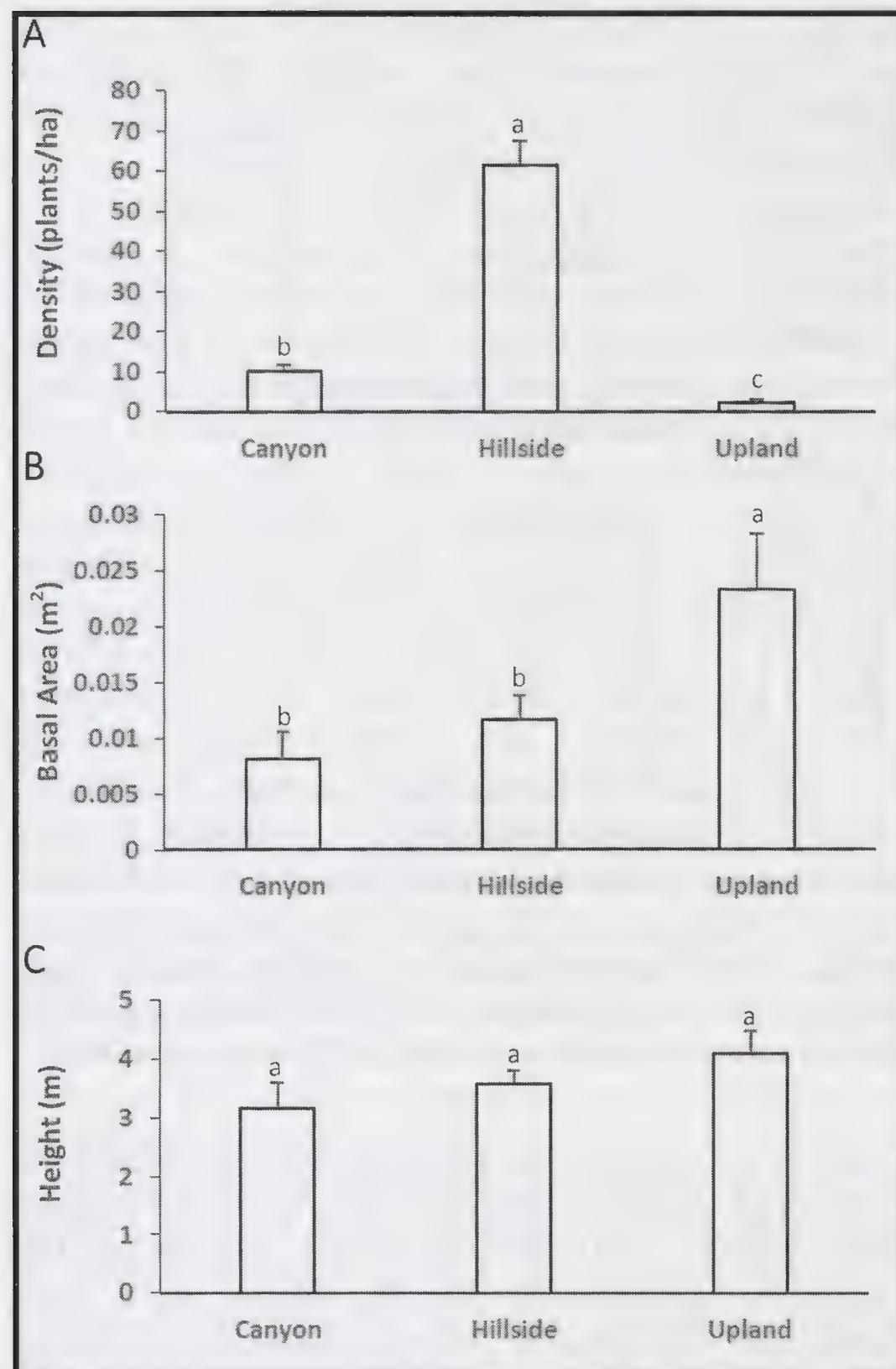


FIG. 3. Comparisons of mean (± 1 SD) *Arbutus xalapensis* traits by habitat type. (A) density, (B) basal area, and (C) tree height. Sample size was 98 plants. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

RESULTS

Community Comparisons

There was a significant difference in *A. xalapensis* density among the three communities studied (Kruskal-Wallis Test, $\chi^2 = 58.38$, $df = 2$, $P < 0.001$, Fig. 3A). Dunn's post hoc test revealed differences between canyon and hillside communities ($Z = -4.904$, $P < 0.001$), canyon and upland communities ($Z = 2.026$, $P = 0.043$), and hillside and upland communities ($Z = 7.564$, $P < 0.001$) (Fig. 3A). Mean density ($\pm SD$) was 10 ± 5 plants/ha in the canyon bottoms, 61 ± 38 plants/ha in the hillside and 2 ± 3 plants/ha in the upland or hill top communities.

A significant difference was also found in basal area among the three communities (Kruskal-Wallis Test, $\chi^2 = 10.19$, $df = 2$, $P = 0.006$, Fig. 3B). Dunn's post hoc test showed differences between the canyon and upland communities ($Z = -2.928$, $P = 0.003$), as well as between hillside and upland communities ($Z = -2.818$, $P = 0.005$), but not between canyon and hillside communities ($Z = -0.828$, $P = 0.408$) (Fig.

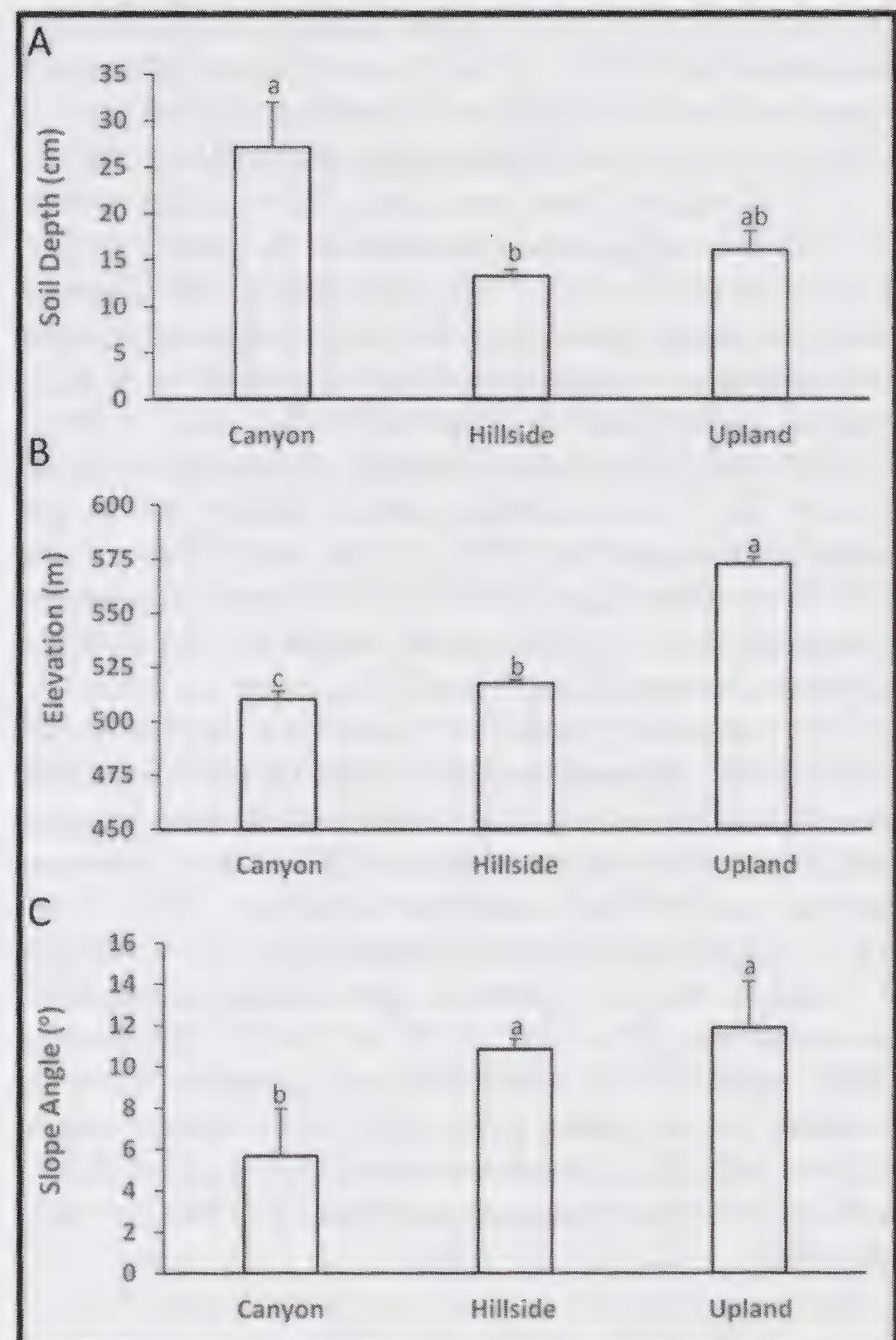


FIG. 4. Comparison of mean (± 1 SD) *Arbutus xalapensis* sites by habitat type. (A) soil depth, (B) habitat type, and (C) slope angle. Sample size was 98 plants. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

3B). Greatest *A. xalapensis* basal area was in the hilltop communities at 210 ± 190 cm/plant, followed by the hillside at 110 ± 170 cm/plant and canyon bottom communities at 80 ± 100 cm/plant. The data suggest an overall trend of increasing basal area from the canyon bottom communities to the upland communities (Fig. 3B).

Plant height did not significantly differ among the three communities studied (Kruskal-Wallis Test, $\chi^2 = 3.82$, $df = 2$, $P = 0.148$). Though no statistical differences were found, a trend of increasing height can be seen with shortest plants occurring within canyon bottom communities (3.2 ± 1.8 m) and the tallest (4.1 ± 1.7 m) occurring within upland communities (Fig. 3C).

A marginally significant difference in soil depth was found among the three *A. xalapensis* communities (Kruskal-Wallis Test, $\chi^2 = 5.96$, $df = 2$, $P = 0.051$) (Fig. 4A). Dunn's post hoc test showed a statistically significant difference between the canyon and hillside communities ($Z = 2.261$, $P = 0.024$), but not between canyon and upland communities ($Z = 0.686$, $P = 0.493$) or hillside and upland communities

($Z = -1.407$, $P = 0.159$). Canyon communities had the deepest soil (27.2 ± 2.1 cm), followed by upland communities (16.0 ± 8.6 cm) with the shallowest soil (13.3 ± 5.5 cm) in hillside communities (Fig. 4A).

For elevation there was a significant difference in the three *A. xalapensis* communities (Kruskal–Wallis Test, $\chi^2 = 49.39$, $df = 2$, $P = 0.010$) (Fig. 4B). Dunn's post hoc test revealed differences between canyon and hillside communities ($Z = -2.546$, $P = 0.011$), canyon and upland communities ($Z = -6.711$, $P < 0.001$), and hillside and upland communities ($Z = -5.810$, $P < 0.001$). The highest elevation was in the upland communities (573 ± 14 m) followed by hillside communities (518 ± 14 m) and the lowest elevation (510 ± 16 m) was found within canyon bottom communities (Fig. 4B).

There was a significant difference in slope angle in the three *A. xalapensis* communities (Kruskal–Wallis Test, $\chi^2 = 12.12$, $df = 2$, $P < 0.005$) (Fig. 4C). Dunn's post hoc test demonstrated differences between canyon and hillside communities ($Z = -3.367$, $P < 0.01$), canyon and upland communities ($Z = -2.789$, $P < 0.01$), but not between the hillside and upland communities ($Z = -0.112$, $P < 0.05$). The lowest slope angle ($5.59^\circ \pm 2.28^\circ$) was found in canyon bottom communities (Fig. 4C). The highest slope angle was in the upland communities ($11.89^\circ \pm 2.26^\circ$) followed by the hillside communities ($10.84^\circ \pm 0.51^\circ$) (Fig. 4C).

Geological Comparisons

The mean basal area ($\pm SD$) of *A. xalapensis* was significantly higher on the Fort Terrett member substrates, 230 ± 220 cm^2/plant , compared to the Upper Glen Rose Formation substrates, 110 ± 150 cm^2/plant (Mann-Whitney U-Test, $W = 632.5$, $P = 0.029$, $n = 128$) (Fig. 5A). Significant differences were found between the geology substrates regarding density of *A. xalapensis*. The Fort Terrett member of the Edwards limestone had an *A. xalapensis* density of 2 ± 3 plants/ha and plants on the Upper Glen Rose had a density of 16 ± 7 plants/ha ($W = 1702.5$, $P < 0.001$, $n = 128$) (Fig. 5B). Mean height was higher among Fort Terrett member of the Edwards limestone sites, 3.93 ± 1.82 m, compared to Upper Glen Rose sites, 3.41 ± 1.57 m, but not significantly different ($W = 792$, $P = 0.289$, $n = 128$). Elevation was higher on Fort Terrett sites, 574.63 ± 12.69 m, compared to Upper Glen Rose sites, 515.71 ± 13.01 m ($W = 640$, $P = 0.031$, $n = 128$). Mean soil depth was deeper in Upper Glen Rose sites compared to Fort Terrett member of the Edwards limestone sites (15.32 ± 11.17 cm and 14.09 ± 4.42 cm, respectively) but not significantly different ($W = 814.5$, $P = 0.367$, $n = 128$).

DISCUSSION

Juniperus-Quercus woodlands are a major component of the Edwards Plateau ecological region of



FIG. 5. Comparison of mean (± 1 SD) *Arbutus xalapensis* (A) basal area and (B) density by geologic substrate type. Sample size was 128. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

Texas (Van Auken et al. 1979; Riskind and Diamond 1988; Van Auken 1988; Russell and Fowler 1999; Van Auken 2018). Many studies examining the vegetation composition of this region have been conducted, and though *Arbutus xalapensis* is known to occur in the region, it has yet to be reported in ecological studies and its community density and basal area have not been reported. Thus, where it specifically occurs has really not been thoroughly investigated (Van Auken et al. 1979; Van Auken 1988; Sorensen 1995; Van Auken et al. 2017; Van Auken 2018). *Arbutus xalapensis* is an evergreen tree that is known to have disjunct populations in Texas, and is found in various places in Mexico, and Central America (Amos and Rowell 1988; Tirmenstein 1990). Distribution of *A. xalapensis* is said to occur in canyon and creek bed habitats as well as on hillsides (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). This information, however, seems mostly anecdotal and vague. Almost all previous reports are notable for their lack of quantitative vegetation data, but attempt to place species, including *Arbutus xalapensis*, in an ecological framework based on plant occurrence and observation (Gehlbach 1967).

The present study examined three community types in which *A. xalapensis* has been observed within portions of central Texas. It was expected that *A. xalapensis* would be largest and have the highest density within the hillside communities. This did not occur. We found the largest *A. xalapensis* plants in the hilltop *Juniperus* communities. However, highest density of *A. xalapensis* was in the hillside communities. In the Guadalupe Mountains of west Texas and New Mexico, *A. xalapensis* has been reported in

canyons with *Acer grandidentatum* and *Quercus muehlenbergii* Engelm. as dominant species and *Juniperus deppeana* Steud., *Quercus grisea* Lieb., and *A. xalapensis* as important contributors to the nearly closed canopy (Gehlbach 1967). Also, in west Texas, *A. xalapensis* is widespread in the Davis Mountains, including wooded canyons, mountain slopes and drainages, but not specific habitats and no ecological characteristics are presented (Powell 1998). In southwest Arizona, the Arizona madrone (*Arbutus arizonica* Sarg.) is reported in *Quercus* woodlands (Epple and Epple 1995), in pine-oak woodlands and canyon bottoms in the pine-oak forest zone (Gehlbach 1981; Barton 2005; USDA NRCS 2016). The Pacific madrone (*A. menziesii* Pursh) is present from southwestern British Columbia into southern California, including the Sierra Nevada of central California (Whitney 1998). It is described from a number of habitats including foothills, upland slopes and canyons in oak and coniferous forests, where it is often in open forests, rocky slopes, ravines and also the understory. These reports make it difficult to predict where these species of madrone should be found in the environment, or if one or all madrone species are overstory or understory species.

Differences in geological substrates seemed to explain some of these dissimilarities, or differences at least, observed among the central Texas *A. xalapensis* populations. The Fort Terrett member of the Edwards limestone is a very hard limestone, with mostly shallow soils, and it occurs on hilltops in most of the ABK natural area and other areas in central Texas (Riskind and Diamond 1988; Woodruff et al. 1994). It appears that the *A. xalapensis* trees that we found on hilltops, on hard Edwards limestone established a long time ago because of their size. They are large trees and possibly established in limestone cracks where additional soil accumulated (Weaver and Jurena 2009). This is supported because mean soil depth where the trees were found was 16.0 cm, whereas general upland soils were 10.8 cm deep (Van Auken et al. 2017). Soils of the Upper Glen Rose Formation were deeper, holding more water, and supporting a higher density of *A. xalapensis* trees (Van Auken et al. 1981 and present study).

In several instances, results from the current study differed from existing reports (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). We found *A. xalapensis* populations in different habitats and with different ecological characteristics than some of the literature suggested (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012). Overall, basal area and height were both less than described in previous reports, which could be explained by collection site differences. In addition, the elevation range at which *A. xalapensis* was found in this study (493–589 m) was considerably lower than suggested in previous reports (1219–

3400 m) (Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015), but within the elevation range given in the Flora of North America (300–2200 m) (Sorensen 2009).

The density of *A. xalapensis* was highest in hillside communities, followed by canyon communities, where *A. xalapensis* was noted to occur, but *A. xalapensis* was also found in upland communities, where it was not reported previously (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). The differences in the overall population size and distribution may not refute previous reports, but the results show that the central Texas populations are somewhat different than other populations previously described (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012). This may be possible because the area of study is different or more care was taken noting community or habitat type in the current study than in previous studies. Some of the parameters collected, especially height and basal area, may be used in the future to approximate the age of *A. xalapensis*, as has been done for other species (Ferguson and Carlson 2010).

Higher *A. xalapensis* density was found below a woodland canopy, where reduced light levels were previously recorded (Van Auken et al. 2017). Lower light levels have been shown to be important in the growth and development of *A. xalapensis* juveniles, but higher light levels seem required for the growth and development of mature trees (suggested by Whitenberg and Hardesty 1978). *Juniperus ashei* and other *Juniperus* species seem to germinate, establish and grow best in low light conditions, while adults seem to require full sun (Van Auken et al. 2004; McKinley and Van Auken 2005; Kane et al. 2011). The same may be true for *A. xalapensis*.

Deepest soils were found within the canyon communities, but hillside soils were shallower than upland soils. Mean soil depth, within one meter of *A. xalapensis* individuals, within canyon and upland communities in the present study were deeper than the soil depth recorded within similar canyon and upland communities in a previous study (Van Auken et al. 2017). Deeper soils may lead to increased retention of soil water and possibly other soil nutrients, and *A. xalapensis* establishing, growing, and surviving in deeper pockets of soil may be due to water-related stresses in associated shallower soil (Van Auken et al. 1981; Weaver and Jurena 2009; Geroy et al. 2011). This would not seem to work in the canyon communities because of the lower light levels below the overstory canopy (Van Auken et al. 2017).

This study showed that the central Texas populations of *A. xalapensis* are different than other populations previously described (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). Within the Edwards Plateau, *A.*

xalapensis appears to be shorter and with less girth than in other portions of its range. This may point to the already documented variability within the species or it may necessitate examining population genetics, competition, light requirements, or soil nutrient and water availability more carefully (Barbour et al. 1987). The analysis of density between habitats showed that *A. xalapensis* clearly favors lower slopes and does not readily establish in flat upland communities with shallow soils or canyon communities with deeper shade. More juvenile *A. xalapensis* plants than mature ones (not shown) suggest a potentially expanding population (Harper 1977; Barbour et al. 1987), which would be very interesting. It is also possible that *A. xalapensis* establishment only occurs sporadically or episodically.

We have barely scratched the surface concerning the ecology and distribution of *A. xalapensis* in south-central Texas. Other studies are needed to understand the ecological requirements of this species. These studies are necessary for prediction of future population structure of this species, especially demographic changes. In addition, how does the Texas *Arbutus* compare with the California, Arizona, Mexican and Central American madrones? No one knows the answer, but this information would be important for future conservation of these species.

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THE TAXONOMY OF *CHENOPodium Hians*, *C. INCOGNITUM*, AND TEN NEW TAXA WITHIN THE NARROW-LEAVED *CHENOPodium* GROUP IN WESTERN NORTH AMERICA, WITH SPECIAL ATTENTION TO CALIFORNIA

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ABSTRACT

In our search to document the fruits of *Chenopodium* L. taxa in North America to assist identifications, and after demonstrating fruits to be stable and diagnostic, we here focus on the some of the “narrow-leaved” group taxa prevalent in the western part of the continent. For this study, we sampled and classified, employing fruit characters as the leading criteria for categorization, more than 500 herbarium collections of *Chenopodium* of western North America, with a special focus on California. We concentrated only on taxa with fruits with adherent pericarp and lanceolate to lance-ovate, entire, un-lobed, or basally lobed leaves. Here, we recommend the recognition anew of *C. incognitum* Wahl as a separate species from *C. hians* Standley and 10 new species of *Chenopodium* in California and nearby states of western North America. The recognition of these taxa contributes to an ongoing study of the taxonomy of native *Chenopodium* in California, where an in-depth local taxonomic treatment of the genus has never before been presented. Our classification is supported both by biogeographical distribution and morphological characters. Taxonomic keys are provided.

Key Words: California, Chenopodiaceae, *Chenopodium*, fruits, North America, taxonomy.

Comprehensive phylogenetic analyses (Fuentes-Bazán et al. 2012a, b) have provided a revised classification of *Chenopodium* L. s.l., recognizing six independent lineages: *Chenopodium* s.s., the largest and most diverse clade, *Blitum* L., *Chenopodiastrum* S. Fuentes, Uotila, & Borsch, *Dysphania* R.Br., *Lipandra* Moq., and *Oxybasis* Kar. & Kir. These molecular studies are congruent with morphological features as well. However, *Chenopodium* s.s. includes many incompletely defined and poorly known taxa, reaffirming its reputation as a difficult genus and more recently again, as a very challenging group to resolve taxonomically (Sukhorukov et al. 2018).

The notorious difficulty in distinguishing *Chenopodium* using vegetative characters stems both from the early dehiscence of the plant’s primary leaves, which are often shed prior to fruiting and absent in many collections, and from a plant architecture that varies considerably with environmental factors. These two issues are further complicated by the high plasticity of the leaves, to the point that different taxa often appear vegetatively similar with few other characters that can aid in identification. Therefore, the assessment of observable differences in vegetative characters has remained a highly subjective activity. In addition, many *Chenopodium* species are also of intermittent or episodic appearance (Jellen et al. 2011, Benet-Pierce, personal observations), fairly rare, and poorly known. It is still inconclusive if species of *Chenopodium* are highly dependent on colonizing disturbed habitat only and disappear after more established plant species have gained a permanent foothold, or if they also occupy a specialized

ecological niche in a climax community (Ladyman 2006).

All these difficulties have not made *Chenopodium* particularly popular among botanists; thus, comprehensive treatments of *Chenopodium* in North America have been few. Standley (1916, 1917) produced probably the most extensive and thorough of the early *Chenopodium* treatments. Standley (1917) described many new species of the genus from Arizona, New Mexico, and Nevada, but he then admitted:

“It is unfortunately true that the North American species are still poorly understood, and that a wholly satisfactory arrangement of them is apparently not to be secured at present”

(pp. 413).

This outlook was further supported in Aellen’s (1929) seminal *Chenopodium* study, which he entitled only a “Contribution...” and by Aellen and Just (1943), who indicated its incomplete nature in stating:

“Obviously many American records will have to be added in the future.”

(pp. 47).

Similarly, Wahl (1954) called his major study solely “A Preliminary study of the Genus *Chenopodium* in North America” and he mostly focused on eastern North American species. While Wahl did add two new species, *Chenopodium incognitum* Wahl and *C. foggii* Wahl, to his taxonomic treatment and did collect in California, there was scant additional examination of *Chenopodium* in the state. In addi-

tion, most of Standley's (1916, 1917) species were never confirmed as occurring in California.

The next, and most recent comprehensive treatment of *Chenopodium*, is that in the Flora of North America (Clemants and Mosyakin 2003). This treatment brought new clarity to the genus. However, without presenting new criteria for their evaluation, many taxa were placed in synonymy (e.g., *C. incognitum* see below), and the descriptions of most recognized entities were left still too vague to permit precise identifications.

Except for our very recent studies (Benet-Pierce and Simpson 2010, 2014, 2017), no other native North American *Chenopodium* species had been described in the last 50 yrs, even with an enormous number of collections. Instead of additions, some taxa that had previously been described and named, fell into synonymy, such as *Chenopodium incognitum*, which has generally been viewed as a synonym of *C. hians* Standl. (e.g., Clemants and Mosyakin 2003). Many of the species in the *C. neomexicanum* Standl. complex, described by Standley and Aellen had also taxonomically disappeared, in part due to the difficulty that botanists had to tell the plants apart conclusively. We showed this was rectifiable with the use of fruits and seeds (Benet-Pierce and Simpson 2017).

Standley and Aellen were both well aware of the importance of fruit characters to aid on the discrimination and description of species, as they used fruit and seed traits in their descriptions. Wahl, in particular, insisted on the importance of fruit characters considering them "of primary significance in 'separating interbreeding populations'. This is evident because of the relative distinctiveness between the fruits of individual species and because other characters are correlated with these fruit differences ..." (Wahl 1954)

(p.3).

Historically though, very few traits of fruits and seeds of *Chenopodium* had been known or described in the earlier treatments or by the botanists that followed. The intensive sampling of fruits and seeds in our ongoing study of *Chenopodium* taxonomy has shown us that there are a great number of characters with sufficient diagnostic features to be able to characterize taxonomic entities in the genus. These characters have the necessary stability and diagnostic power that *by themselves* can sufficiently assist or even permit the identification of taxa. This has been an unexpected and extraordinary discovery, the equivalent of the lucky find of a Rosetta Stone for this difficult genus, in which the vegetative characters are so challenging to assess. This new perspective has great potential for improving *Chenopodium* taxonomy and it is not surprising new species in California are only now being brought to light.

Improving the taxonomy of *Chenopodium* will provide a more accurate categorization of range of biodiversity, which will aid in the efforts of other scientists (e.g., those working on the DNA sequenc-

ing of *C. berlandieri* Moq). This widely distributed taxon, reportedly twice domesticated in the North American continent and part of native eastern North American crop complex, is considered a critical potential genetic resource for adaptive improvement the South American crop quinoa (*Chenopodium quinoa* Willd.), which has worldwide importance (Jarvis et al. 2017; Brenner et al. 2019).

With our ongoing goal of clarifying the taxonomy of *Chenopodium* of the western North America, where so many species occur, we here focus on employing fruit characters, in addition to vegetative features, on a group treated before under the designation "narrow-leaved". This term was applied to four to seven species by workers in the complex (Crawford and Reynolds 1974; Crawford 1975; Crawford and Julian 1976; Crawford and Wilson 1979; La Duke and Crawford 1979) referring to taxa with marginally entire, unlobed or basally lobed, lanceolate or lance-ovate leaves. We have used fruits as the primary classification tool, as they provide the best characters for recognizing independent taxonomic entities. Once diagnosed, these entities can be correlated with vegetative features and biogeographic ranges. These morphological studies are a necessary preamble to future molecular and phylogeographic studies in the complex.

Of the species generally included in this narrow-leaved group, we concentrate here only on the species with an adherent pericarp, which have been identified in California and most western states as *Chenopodium hians* Standley, *C. incognitum* Wahl (if recognized), or often as *C. atrovirens* Rydberg plants with adherent pericarp. The pericarp, when adherent, is highly informative, yielding a number of diagnostic features; thus, it is beneficial to begin by segregating these taxa. Of the other species traditionally included in this group, *Chenopodium inamoenum* Standley (considered by some to be synonymous with *C. leptophyllum* (Moq.) Nutt. ex. S.Watson and very occasionally with *C. hians*) has linear leaf blades and much smaller sized fruits. Thus, we have provisionally grouped *C. inamoenum* into to what we now call the *C. leptophyllum* aggregate, a loose assemblage of entities with free or adherent pericarp, fruits smaller than 7 mm and linear leaf blades, to be studied at a later date. *Chenopodium atrovirens* Rydberg (occasionally identified as *C. hians*) and *C. pratericola* Rydberg, both with more ovate but entire and basally lobed leaves, do not have an adherent pericarp; these taxa will also be the focus of study at a later date, when taxa with non-adherent pericarp will be treated. *Chenopodium pratericola* Rydb. is here defined under an aggregate classification as well, as we are seeing that it has been used as an umbrella category for more than one taxon. The remaining species with a non-adherent pericarp, *Chenopodium desiccatum* A. Nelson, has been treated already (Benet-Pierce and Simpson 2014). The study for this paper excludes all taxa with toothed leaves, among these *Chenopodium album* L. and *C. strictum* Roth,

which have been rather loosely classified in North America and are in need of extensive taxonomic work. Using fruit characteristics may prove highly advantageous to improve the taxonomy of these widespread taxa as well.

METHODS

Fruits were examined of more than 550 *Chenopodium* herbarium collections from western North America (with emphasis on California) of members of the “narrow-leaved” complex, but with an adherent pericarp. These comprised specimens identified as *Chenopodium hians*, *C. incognitum*, or *C. atrovirens* with an adherent pericarp (noting that some previous workers considered pericarp adherence to be variable in the latter species). Specimens were obtained from herbaria at ALA, ARIZ, ASC, ASU, BABY, BM, BRIT, BRY, CAS/DS, CDA, CHSC, COLO, DAV, DES, G, GH, ID, JEPS, K, MO, MONT, MONTU, NMC, NY, OBI, ORE, OSU, P, PAC, RENO, RM, RSA/POM, SBBG, SD, SDSU, TEX, UBC, UC, UCR, UNM, UNLV, US, UTEP and WTU (Thiers 2019). Around 280 specimens were from the western United States, but outside California, and a larger number (around 300) from California alone. We also widely collected across eastern California, where all of these species occur (see Figs. 1–6, below). Photographs were taken of all herbarium specimens examined; high-resolution scans were made of some specimens on loan to the San Diego State University Herbarium (SDSU).

Fruits were removed and placed on double-stick tape affixed to a labeled microscope slide, all housed at SDSU. Fruits were studied under a high-powered (40x) dissecting microscope and qualitatively evaluated for differences in size, shape, color, and sculpturing pattern. As the study progressed, groupings were made of specimens with highly similar fruit morphology. This was done only after many specimens were comparatively examined in order to establish stable and continuously occurring differences and similarities in pattern and form, while considering natural variability as well. In addition, fruits from the type specimens of *Chenopodium hians* and *C. incognitum* (see below) were similarly examined for comparison with those from other specimens. The fruits of examined specimens were subsequently classified as belonging to either of the aforementioned taxa or as being unique and representing a new taxon.

After the classification by fruit morphology was well established, vegetative characterizations of specimens were made for all designated taxa. These included evaluation of stems, including stem diameter, height and branching pattern, and of leaves, both primary leaves (those arising basally mostly from the primary axis, but often missing in a specimen) and secondary leaves (those arising from more apical, secondary branches) when present. Similarities were noted among vegetative features of

a given taxon and descriptions were made. We emphasize that our classification is based above all on fruit differences, as they have proven to be robust in segregating taxa adequately. Extreme caution was made to describe only what we believe to be well-supported entities.

From the establishment of these taxonomic entities, we proposed to designate ten of these as species new to science. For all taxa, the fruits were photographed in top, bottom, and side views using a Visionary Digital BK Plus Lab System high-resolution photomicroscope (Dun, Inc. Palmyra, VA). Type specimens were selected and imaged for the ten new taxa (Figs. 1–3). Formal names and descriptions are presented below in the Results section. A website has been developed for *Chenopodium* in North America which now incorporates the narrow-leaved species included in this paper. This website provides images of numerous additional specimens and fruits for examination of features within taxa (Benet-Pierce 2014 onwards; <https://plants.sdsu.edu/chenopodium>).

RESULTS AND DISCUSSION

The fruits from the type specimens of the described taxa within the narrow-leaved and adherent pericarp group, *C. hians* and *C. incognitum*, were unfortunately not in very good condition. The examination of many specimens was necessary before their fruit features could be fully characterized and employed for classification. As mentioned earlier, *C. incognitum* has been considered a synonym of *C. hians* in recent treatments. However, we have determined that these two species are well differentiated, both in their fruits and vegetative characters. After studying hundreds of collections, we here document the diagnostic fruit for each taxon, their vegetative features, and their geographical distribution. We have also posted numerous specimen images online, so that their vegetative and fruit characteristics can be easily appreciated (Benet-Pierce 2014 onwards; <http://www.sci.sdsu.edu/plants/chenopodium/index.html>). We note that only two years after having been able to fully delimit *Chenopodium incognitum* from *C. hians*, we found the first fruit with an almost completely intact pericarp of the former in the packet of a duplicate collection saved by Paul Aellen at (G), many years before Wahl had designated a simultaneous collection as the type for that species. We had found no intact fruits earlier at the National Herbarium (US). In addition to its different fruit morphology, and vegetative aspect, *C. incognitum* appears to have a different and much wider geographic range than *C. hians* (see species descriptions below). Both species are well illustrated on our website.

With the firm diagnosis of these two described taxa, it became evidently clear that most of the California specimens that had been previously identified as *C. hians*, *C. incognitum*, or *C. atrovirens*

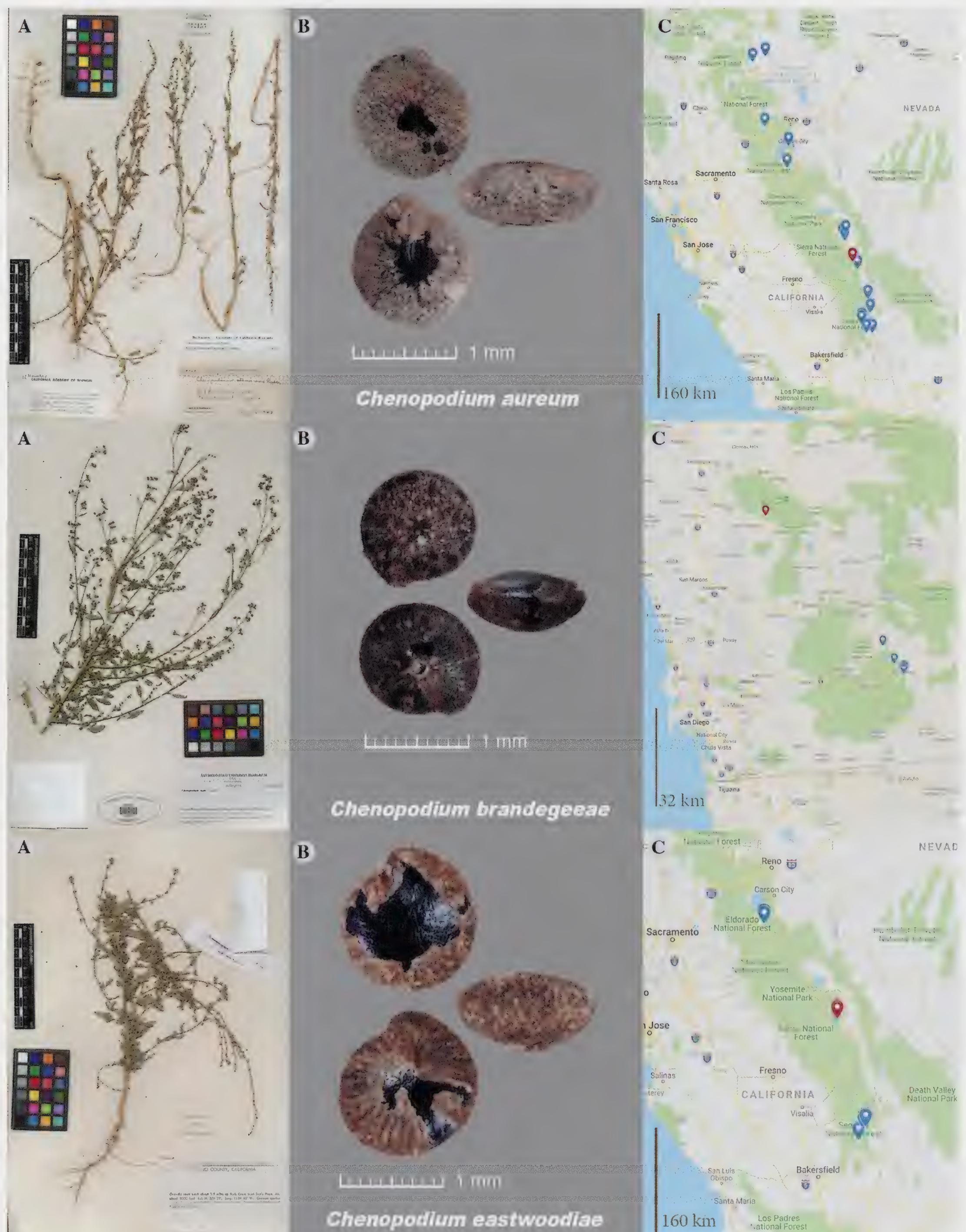


FIG. 1. A. Type specimen; B. Fruit images, with top of fruit image at left, bottom below and side view with bottom below at right; C. Map of geographical distribution for each taxa. Top row: Designated Type of *Chenopodium aureum* CAS 342155 Howell 24151 duplicates at CAS, G & RSA herbaria. Fruit images from SDSU 22226, Benet- Pierce & J. P. Pierce 665 & side view SDSU 22230 Benet-Pierce & J. P. Pierce 669. Map: CA, ID & NV. Center row: Designated Type *C. brandegeae* SDSU 19747, Benet-Pierce & J.P. Pierce 336. Fruit images SDSU 19726, N.B. Pierce & J.P. Pierce 319. Map: CA: San Diego County, CA. Bottom row: Designated Type *C. eastwoodiae* John H. Thomas 9772, DS 577435. Fruit images SDSU 22005 Benet- Pierce & J. P. Pierce 403 El Dorado Co. CA. Map: CA: El Dorado, Mono and Tulare counties.

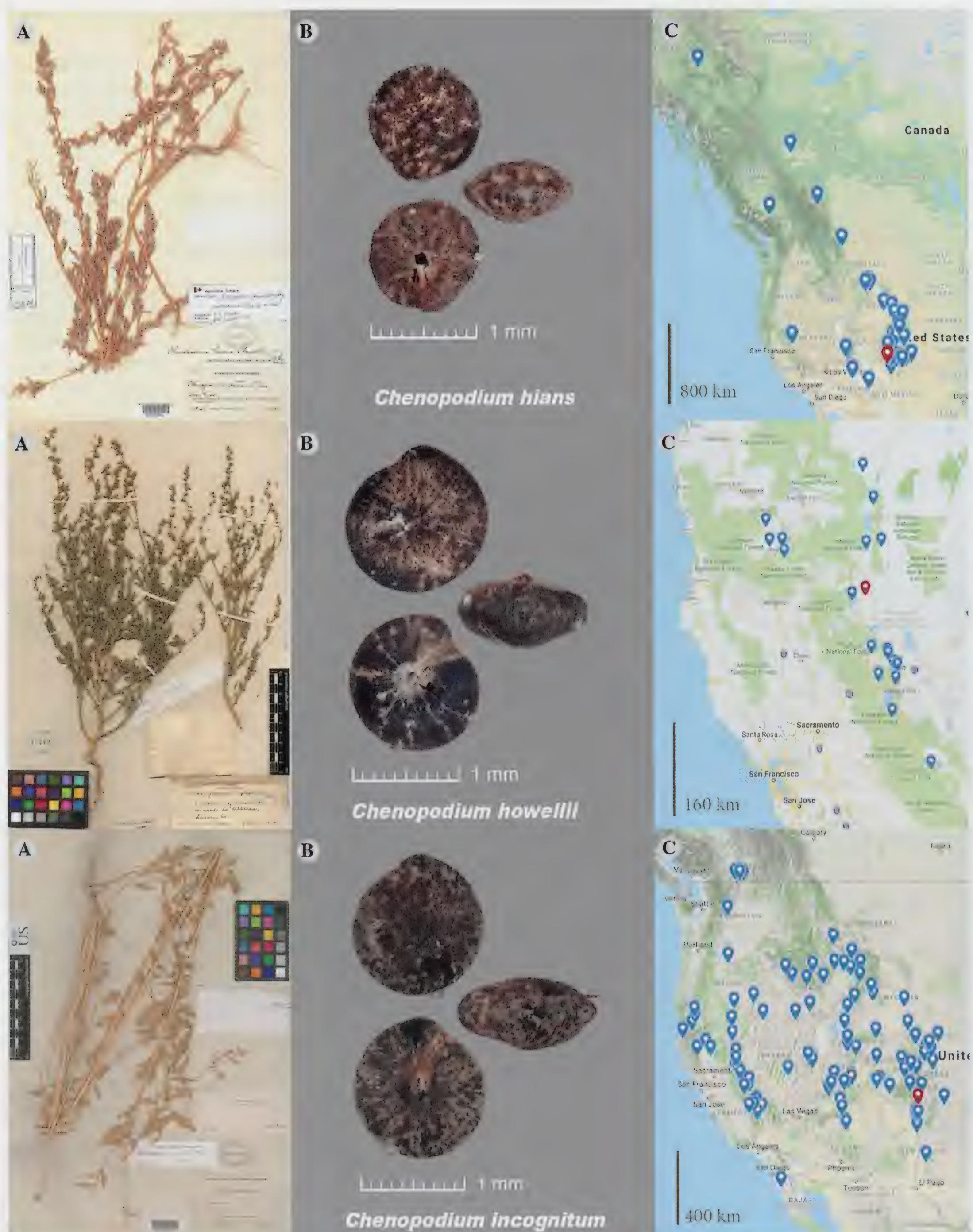


FIG. 2. A. Type specimen; B. Fruit images, with top of fruit image at left, bottom below and side view with bottom below at right; C. Map of geographical distribution for each taxa. Top row: Type specimen of *C. hians* Standley, US 687056 P. C. Standley 8129. Fruit images GH Porter & Porter 9491 Albany Co, WY with many duplicate specimens. Map: US: AZ, CO, MT, NM, NV, UT, WY and in British Columbia and the Yukon Territory in Canada. Center row: Designated Type *C. howellii*, CAS 217242 John Thomas Howell 11900 Lassen Co. CA. Fruit images WTU 20545 Morton E. Peck 15489 (DS 171540!) Lakeview Co. OR. Map: CA: Alpine, El Dorado, Lassen, Modoc, Mono, Plumas, Siskiyou and Tulare counties. NV: Washoe & Carson City. OR: Lakeview County. Bottom row: Type specimen of *C. incognitum* Wahl, US 689661 Standley & Bollman 11012, Rio Arriba Co. NM. Fruit images G 20594 Dup. coll. of Standley & Bollman 11014, Rio Arriba Co., NM. Map: US: AZ, CA, CO, ID, MT, NM, NV, OR, UT WA and WY in British Columbia, CAN.

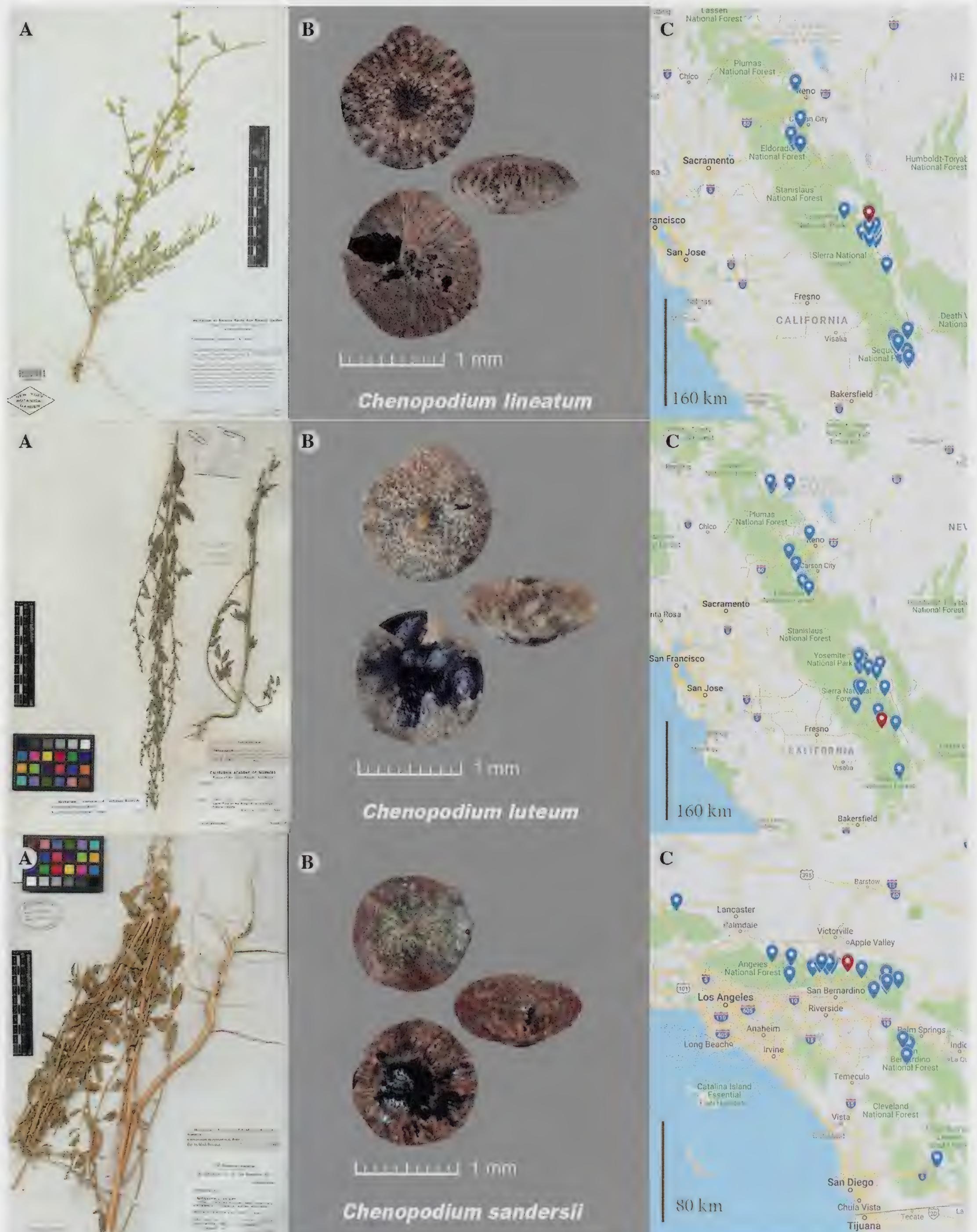


FIG. 3. A. Type specimen; B. Fruit images, with top of fruit image at left, bottom below and side view with bottom below at right; C. Map of geographical distribution for each taxa. Top row: Designated Type for *C. lineatum* NY 801483 M. Honer 1476 Mono Co (RSA-POM 680706!) CA. Fruit images: RENO 24425 M. Williams 72-71-1, Washoe Co. NV (CAS 637629!) Side view: Benet- Pierce & J. P. Pierce # 358 (SDSU 21937!) Map CA: Alpine, El Dorado, Inyo, Mono, and Tulare counties. Center row: Designated type for *C. luteum*, CAS 457912 Javier Peñalosa 2121, Fresno Co. CA. Fruit images SDSU 21993 Benet-Pierce & J. P. Pierce 391, 2011, El Dorado Co. CA Map: CA: El Dorado, Fresno, Inyo, Lassen, Mono, and Tulare counties. Bottom row: Designated Type *C. sandersii* UCR 100144 Scott White 1852 & C. McGaugh & K. Beanan, San Bernardino Co. CA. Fruit images: RSA 628598 A.C. Sanders 14964, San Bernardino CA (UCR 83371!) Map: CA: LA, Riverside, San Bernardino and San Diego counties.

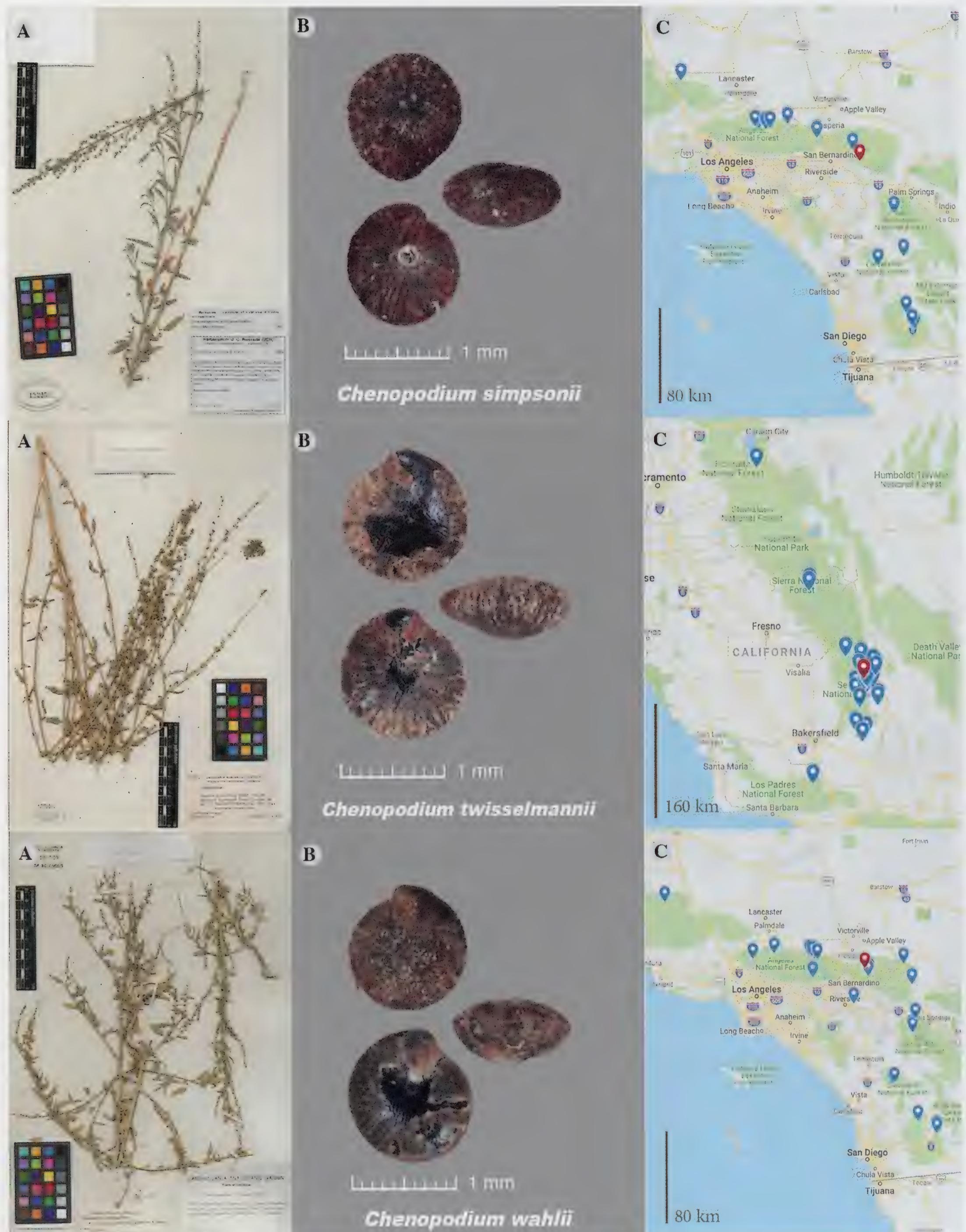


FIG. 4. A. Type specimen; B. Fruit images, with top of fruit image at left, bottom below and side view with bottom below at right; C. Map of geographical distribution for each taxa. Top row: Designated Type of *C. simpsonii* UCR 132956 A. Sanders 14159, San Bernardino, CA. Fruit images: SD 257942 S. M. Leininger 274, San Diego Co. CA. Map: CA: Los Angeles, Riverside, San Bernardino and San Diego counties. Center row: Designated Type for *C. twisselmannii* PAC 81227, grown from fruits CAS 637604 Howell & True, 43934; duplicate PAC 82867, Tulare Co. CA. Fruit images CAS 390819 coll. P.H. Raven7914, Fresno Co. CA. Map: CA: High altitude meadows in Fresno, Inyo, Kern and Tulare counties. Bottom row: Designated Type for *C. wahlii* CAS 438720 Peter H. Raven 16726 dups. GH, RSA, SD and UC, San Bernardino Co. CA. Fruit images Coll. J. Hirshberg 2527, SD 235121, and 2526, SD 235120, San Diego Co CA. Map: CA LA, Riverside, San Bernardino, San Diego, and Tulare counties.



FIG. 5. Fruit images for all the taxa treated in this paper. For each taxon: top of fruit at upper left, bottom at upper right and side view with the top facing upward, below at right.

with adherent pericarp did not fit our diagnoses for those taxa. This is not surprising, given that new species continue to be described for California and given the taxonomic neglect that *Chenopodium* has suffered. Thus, in addition to recovering *C. incognitum* as a species separate from *C. hians*, we recognize here an additional 10 new species of the genus in California and geographically close western states. The absence of detection of these new taxa in the past can partially explain the high rate of misidentifica-

tions of *Chenopodium* specimens in California and the generally misleading sense of much higher intraspecific variation in the genus. Ertter (2000), in her article *Floristic surprises in North America North of Mexico*, argues convincingly that new plant discoveries are still rather common place in the continent and specifically that the exploration and discovery of plants in California is still in ongoing. This seems particularly true for the genus *Chenopodium*, often neglected and underappreciated, and

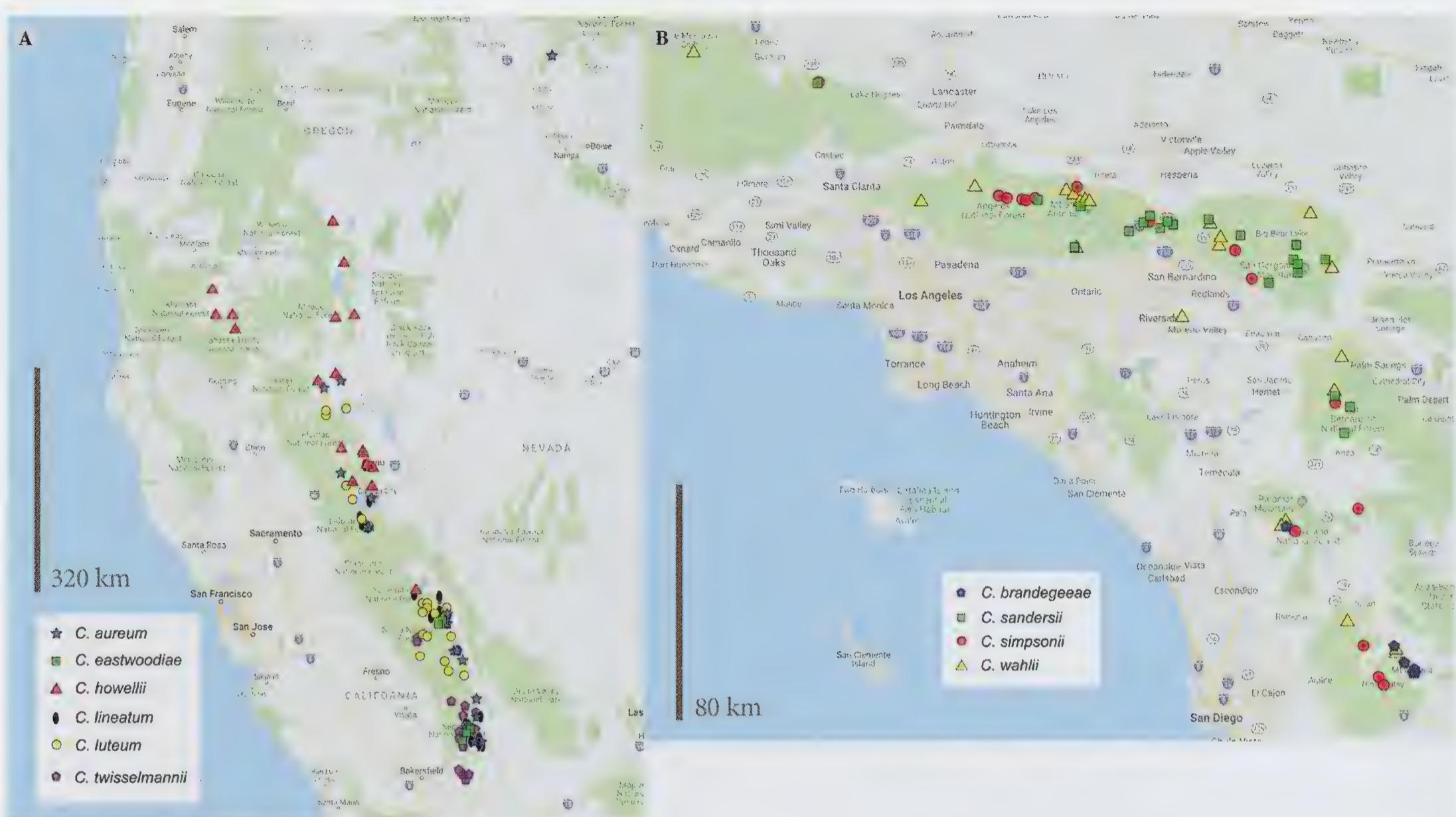


FIG. 6. Geographical distribution maps for all new taxa in this paper. A. Geographical distribution of taxa occurring in northern and eastern CA, ID, NV and OR. B. Geographical distribution of taxa present in southern California.

generally viewed as weeds with the potential for being highly invasive.

As discussed earlier, *Chenopodium* fruits vary in size (diameter), outline shape in face view (oval to round), level of compression as seen in side view (from lenticular to oblate to conical), three-dimensional shape of both the basal face (adjacent to the attachment of the hilum) and upper face (apical or stylar, frequently evident as the sepals open), sculpturing and degree of shine of the seed coat, presence, shape, and thickness of a marked equatorial margin, and characteristics of the pericarp, fundamentally its adherence to the seed, but also its color, pattern, shine, and sculpturing (texture). (Note that the apical pistillate flower of many *Chenopodium* species is larger than lateral fruits. We have occasionally used these apical fruits, when the lateral fruits were unavailable, but did not consider their size.) As this paper deals exclusively with species with an adherent pericarp, its features are of paramount importance. The pericarp is quite diverse, and its characteristics add to other features, especially fruit size, shape, and equatorial margin, offering considerable assistance in identification.

The pericarp is membranous and before maturation most pericarp characters are obscure. Even with the benefit of a vast number of collections, the intact mature fruits of some species were difficult to obtain. Often we worked with less than optimal fruit material, particularly in historical collections. However, taken as a whole, herbarium collections yielded an incredible wealth of material that made possible evaluation of the characteristics and natural variability of both the plants and the fruits, and of their

appearance under different circumstances of maturity, integrity, and decay. As mentioned above, this was particularly important, as the fruit of type specimens of previously described species was generally poor and often partially destroyed (see Benet-Pierce 2014 onwards for images of these). For the species in California, we mostly found intact fruits in relatively new collections. Although fruit character differences may be subtle, once established, they have led us to what we now consider to be different taxonomic entities. Our classifications appear to be well corroborated by both vegetative characters and biogeographical distribution.

Our new taxa descriptions are based on the available specimens to date for a given group. Due to the difficulties of collecting *Chenopodium*, these descriptions may certainly be improved in the future. However, the study of historical specimens of *Chenopodium*, more than five thousand *Chenopodium* specimens across taxa country wide, and over 400 from western North America, including California for this study alone, also has contributed significantly to our understanding of the group, and in our opinion, to the specimens' actualization and increased usefulness as well.

Caution must be exercised when dealing with any of the characters employed here, in that there are always fruits and seeds in every plant that are unviable or deformed. Exceptions based on fruits being defective, have to be allowed as well. For example, some fruits may have lost the pericarp in a species with a normally adherent pericarp. Or, occasionally the pericarp is mostly white and very difficult to differentiate. Or, fruits are rarely oblate

when they are typically conical and vice versa. Or, fruits may often become flatter with age. Too early or very late collections present a problem, as fruits may be immature or decay with age. However, *Chenopodium* is a heavy seeder, which has been advantageous in both old and fresh collections.

We did not consider using scanning electron (SEM) microscopy for our work, as we found sufficient characters that we could easily see with a stereomicroscope and chose to employ the largest number of samples possible to be able to draw firmer conclusions about the vegetative characters, something impractical for SEM. In fact, the elucidation and characterization of color patterns, impossible with SEM, has given us even more characters. We believe that our methods have provided a more reliable path to species identification. SEM may become useful later to confirm or reject affiliations, just as molecular work will be needed to assess phylogenetic relationships.

Previously Described Taxa

Chenopodium hians Standley, N. Amer. Fl. 21(1): 16. 1916. (Fig. 2, top row).—TYPE: USA, New Mexico, Rio Arriba Co., Jicarilla Apache Reservation, near Dulce; elevation 2150 to 2470 m, *P.C. Standley* 8129 (Holotype US 687056!).

P.C. Standley segregated *C. hians* from *C. leptophyllum* due to its foul odor and described it in 1916. We have examined the three specimens Holotype US 687056, US 689474 and US 393385 mentioned by him (Standley 1917), and they all correspond to *C. hians*. This species has never been in doubt, Aellen having added more collections, most of them corroborated by us, with confirmed occurrences in AZ, CO, MT, NM, NV, UT, WY in the U.S. and in British Columbia and the Yukon Territory in Canada (see map in Fig. 2). *Chenopodium hians* plants are seldom branched, 2–3 (up to 4) dm tall. Leaves are unlobed, to 2.5 cm long x ca. 0.5 cm wide. The fruit is small, conical below, with a highly patterned pericarp of minute brown and white papillae. Very rarely, the pericarp is very dark brown, and smooth with a flatter fruit, but with the same patterned pericarp (US 689474, Standley & Bollman 10764). We have confirmed that these two fruit types occur on the same plants, but very seldom (see Benet-Pierce 2014 onwards for images).

Wahl recognized another entity that he found different enough from *C. hians*, occurring in the West, *C. incognitum* (below), while acknowledging that the plants in California of *C. hians* “may consist of more than one recognizable taxon” Wahl (1954, pp. 21) and recommended further study Wahl (1954, pp. 22). Our study confirms this, and many sheets annotated by Wahl as deserving separate recognition, are now being reclassified.

Chenopodium incognitum Wahl (Fig. 2, bottom row).—TYPE: New Mexico, Rio Arriba Co., Pine Woods Vicinity of Brazos Canyon, *P.C. Standley*

P.C. & Bollman 11012, Holotype US 689661! Isotype: G 20594! Duplicate collection *Standley & Bollman* 11014 (G Standley & Bollman! US 689663!).

Herbert A. Wahl (1954) described *C. incognitum* as large plants “3–12 dm tall, branched from base; lf blade ovate to deltoid-ovate 1.5 to 3.5 cm long, unlobed or with basal lobes, pericarp attached to seed and margin rounded.” He chose his type from one of Aellen designated specimens of *Chenopodium standleyanum* Aellen, identified as such when he believed it was also present in the West and to which it resembles. *Chenopodium standleyanum*, however, has a non-adherent pericarp and does not occur in the West. Wahl ascribed many paratypes for *C. incognitum*, and he listed it as occurring in CA, CO, NM, OR, UT, and WY.

Wahl’s description, albeit appropriate, is very brief. Over the years, the identity of *C. incognitum* was in doubt and the name taxonomically disappeared, remaining as synonymous with *C. hians*. The emphasis on unwarranted synonymy has been a common, but disastrous problem for *Chenopodium* taxonomy. Well-delimited taxa have been disregarded when many botanists were unable to distinguish them adequately. We hope to remedy this somewhat by posting many images of every taxon in our website, so researchers can be made well aware of them.

We here confirm the identity of *C. incognitum* Wahl, as different from *C. hians* Standley with plants branched from base, leaves broadly elliptic or trullate, and we document a much broader distribution, having confirmed a great number of Wahl’s records and in addition many more in AZ, ID, MT, NV, WA in the U.S. and to British Columbia in Canada. We believe that *C. incognitum*, with such an extensive distribution, should be fully recognized; it may eventually be found to comprise some local varieties. Its fruits are large (~1.4 mm), oblate and have a pronounced equatorial margin. The pericarp is initially dark with yellow/gold spots, but ages into a dark brown-dark red or brown with yellow cream spots or lines. Many images of both plants and fruits, may be seen in our website (Benet-Pierce 2014 onwards) and many more records are very likely to be found in many herbaria.

New Taxa

The paucity and incomplete nature of the taxonomic treatments of *Chenopodium* in North America have particularly affected California, as no separate examination of taxa or monographic treatment exists for such a large and rich area for this important genus, other than a very general and brief listing of some described species. Traditionally, the main obstacle to more aptly classifying *Chenopodium* has been the fundamental difficulty in conclusively verifying variability within taxa. The diagnostic power of fruit and seed morphology has added a whole new dimension for doing so. The classification

of the fruits with adherent pericarp most associated with *C. hians*, *C. incognitum*, or *C. atrovirens*, sampled from plants of California and from adjoining areas has yielded a number of new species, and now these entities can be segregated and treated.

We describe below these new taxa and their geographic ranges, noting that in the Golden State *Chenopodium* has played us something like a practical joke. Just as brown colors seem to predominate in the pericarp in the *C. neomexicanum* complex (Benet-Pierce and Simpson 2017), with this trend continuing with *C. hians*, the fruits and seeds of the new California taxa show, in addition to brown, mostly gold and yellow tones. We have placed a great number of images of specimens and fruits in our website (Benet-Pierce 2014 onwards) to illustrate the characters, including pericarp colors, of these species. The following proposed taxa all have very different fruits (Fig. 5). In some cases there is some geographical range overlap (Fig. 6), but their vegetative aspect is also quite distinct. Dichotomous keys to these taxa and the rest of *Chenopodium* in California appear in Appendices 1 and 2, below.

***Chenopodium aureum* Benet-Pierce, sp. nov.** (Fig. 1, top row).—TYPE: USA, California, Inyo Co., Big Pines Lake Trail, 8600–9000 ft (2600–2750 m), *John Thomas Howell* 24151, 16 August 1947 (Holotype CAS 342155! Isotypes: G 24151!, RSA 44538!).

Representative paratypes. USA, California, Inyo Co., desert slopes near Big Pine Creek at foot of trail to Big Pine Lakes, elevation 8500 ft (2590 m), *Roxana S. Ferris* 8976 (DS 229804! NY 3337062!). Inyo Co., south side of Wonoga Peak, elevation 9000–9500 ft (2743–2995 m). *John Thomas Howell* 26287 (CAS 356884!). Lassen Co., east of Highway 139, southeast of Eagle Lake. Small, seasonally moist rocky clay flat with burned pine and juniper, elevation 5680 ft. (1731 m.) *B. Corbin* 1114, 2 Oct 2002 (NY 652205! right specimen only). Lassen Co., Horse Lake, *Ynez Whilton Winblad* s.n. (CAS 226930!). IDAHO: Washington Co., sagebrush grass zone at border of Douglas fir and ponderosa pine, Brownlee Ranger Station, elevation 4350 ft (1326 m), *E. B. Caswell* 82 (ID 24601!).

Description. Erect weak reddish annual, usually 4–5 dm high, sparsely branched from base. Leaf blades trullate and basally lobed ca. 2 cm long by .5 cm wide, base cuneate and apex acute. Upper leaves elliptic to lanceolate, ca. 1.3 cm long x 0.4 (–0.3) cm wide, entire and slightly farinose. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 30 cm long, with sessile flowers ca. 1 mm in diameter. Fruits round, lenticular in side view, ca. 1.2 mm in diameter x 0.5 mm thick, acute equatorial margin with pericarp adherent of very tiny papillae golden-beige with some large whitish spots, very shiny.

English diagnosis. *Chenopodium aureum* differs from *C. luteum* in that the latter is a more robust plant with longer secondary leaves and larger, oblate fruits, with yellow pericarp and larger papillae overall (~30 micrometers), not the very minute papillae (~15 micrometers) and shiny golden-beige pericarp of *C. aureum*.

Distribution and habitat. *Chenopodium aureum* occurs as scattered populations in sagebrush country. California: Inyo, Lassen, Mono, Sierra, and Tulare counties. Nevada: Carson City. Idaho: Washington Co.

Phenology. *Chenopodium aureum* appears to flower in July, and is in fruit from August to September.

Etymology. The epithet “*aureum*” is Latin for gold or gleaming. The pericarp of this taxon appears golden and particularly shiny, this golden shine accounting for the epithet name.

Suggested common name. Golden goosefoot

***Chenopodium brandegeae* Benet-Pierce, sp. nov.** (Fig. 1, center row).—TYPE: USA, California: San Diego Co., Palomar Mountain Campground, Palomar Mountain State Park, off Hwy 76, *Benet-Pierce* 336 with J. P. Pierce, 15 October 2010, elevation 5196 ft. (1584 m); (Holotype SDSU 19747!).

Representative paratypes. USA, California: San Diego Co., Laguna Mountains, disturbed area in Burnt Rancheria Campground, *Bell* 360, elevation 6000 ft (1830 m); (SD 144539! & UCR 138368!). San Diego Co., disturbed road edge, Cleveland National Forest, Laguna Recreation Area, near Storm Canyon viewing platform, on east side of Hwy S-1, 0.25 mile north of El Prado campground; geology: granitic; *J. Hirshberg* 1228, (SD 208785!). San Diego Co., Palomar Mountain Campground, Palomar Mountain, elevation 5106 ft (1584 m), *Benet-Pierce* 329 (SD 19738!). San Diego Co., Cleveland National Forest, Laguna Recreation Area, Desert View picnic area on Hwy S-1, 1/2 mile NE of Mount Laguna Post Office and store, disturbed vegetation, island in center of picnic area, elevation 5909 ft (1800 m), *J. Hirshberg* 1229 (SD 208784!).

Description. Erect large annual, 3–10 dm high, sparsely branched. Leaf blades, elliptic or lanceolate, occ. lobed, ca. 4.5 cm long x ca. 1.6 cm wide. Upper leaves lanceolate, narrowly elliptic, 0.9–0.7 cm long, occ. falcate, base cuneate, apex obtuse or widely acute and slightly farinose. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 15 cm. long, with sessile flowers ca. 1 mm in diameter. Fruits lenticular, ca. 1 mm in diameter x ca. 0.5 mm thick, margin acute; pericarp shiny brown or when mature randomly mottled brown and black, very shiny. Seed coat black.

English diagnosis. *Chenopodium brandegeae* is similar to *C. hians* in being a thin upright plant, but differs in it being usually a taller plant with larger lobed leaves and lenticular fruits. The fruits, when mature, have a very shiny black and brown pericarp, and are not conical. It differs from *C. whalii* Benet-Pierce in that *Chenopodium brandegeae* is usually thinner, taller, and a more upright plant with very distinct fruits having shiny pericarp, often reddish brown particularly when young, and papillate, black, and brown when mature.

Distribution and habitat. *Chenopodium brandegeae* occurs as scattered populations in disturbed habitats and favors previously burnt areas in San Diego Co., CA.

Phenology. *Chenopodium brandegeae* appears to flower late July, and is in fruit from late August to November.

Etymology. Named for Mary Katharine Brandegee (1844—1920), an American botanist known for her comprehensive studies of flora in California and curator of the CAS herbarium.

Suggested common name. Brandegee's goosefoot.

***Chenopodium eastwoodiae* Benet-Pierce, sp. nov.** (Fig. 1, bottom row). —TYPE: USA, California, Mono Co., gravelly road bank about 3.5 miles up Rd Creek from Tom's place, elevation 8000 ft (2438 m), common co-occurring species include *Pinus contorta* Douglas ex. Loudon ssp. *latifolia* (Engelm. S.Watson) A.E.Murray, *Artemisia tridentata* Nutt., *Cercocarpus ledifolius* Nutt., and *Populus tremuloides* Tidestr. J. H. Thomas 9772, 14 September 1961 (Holotype: DS 577435! CAS-BOT-BC 460965).

Representative paratypes. USA, California: El Dorado Co. Grass Lake 3rd pull out entrance, elevation 9840 ft (2997 m), Benet-Pierce & J.P. Pierce 403, 2011(SDSU 22005!). El Dorado Co., Grass Lake, 1st turn out, elevation 9833 ft. (2997 m), Benet-Pierce & J. P. Pierce 401 (SDSU 22003!). El Dorado Co., Grass Lake, 3rd pull out entrance, elevation 9833 ft. (2997 m), Benet-Pierce & J. P. Pierce 406 (SDSU 22008!). Tulare Co., stringer on the southwest side of Big Meadow, small, dense, roadside colony on loam and decomposed granite, elevation 8150 ft. (2484 m), Jeffrey pine forest, Twisselmann 15985 (CAS 593848! 637682!).

Description. Erect large branched annual 8–12 dm high, bright green and reddish at maturity. Leaf blades broadly lance-ovate and basally lobed, ca. 3 cm long x 1.2 cm wide, base cuneate and apex narrowly obtuse, entire. Upper leaves elliptic to long narrowly elliptic leaves 3.5 x ca. 0.8 cm. Inflorescences terminal and axillary panicles of glomerate spikes ca. 45 cm. long, with sessile flowers ca. 1 mm in diameter. Fruits very large, 1.4 mm in diameter x 0.8

mm thick, round, oblate, but slightly flatter above, margin round, pericarp adherent, thick lined, reddish brown to whitish gray or yellow gray color.

English diagnosis. *Chenopodium eastwoodiae* appears to be a rare plant, characterized by very large oblate fruits with a distinctively thick pericarp of raised papillate bands when mature. It differs from *C. lineatum* Benet-Pierce, which has a much smaller and rather flat fruit and one in which the pericarp color bands are present from the beginning and mostly colored and hardly raised. *Chenopodium eastwoodiae* is similar to *C. incognitum* in the large lobed primary leaves, but it differs in that the secondary leaves are longer and slender, and its fruits larger and with very different pericarp to *C. incognitum*.

Distribution & habitat. California: El Dorado, Mono, and Tulare counties.

Phenology. *Chenopodium eastwoodiae* appears to flower in July, and is in fruit from August to early September.

Etymology. Named in honor of Alice Eastwood (1859—1953), a prolific collector and researcher of the California Flora, curator of the CAS herbarium, and author of more than 310 scientific papers.

Suggested common name. Eastwood's goosefoot.

***Chenopodium howellii* Benet-Pierce, sp. nov.** (Fig. 2, center row). —TYPE: USA, California, Lassen Co., 5 miles north of Horse Lake on road to Alturas, J. T. Howell 11900, 10 June 1934 (Holotype CAS 217242! Isotype DS 230139!).

Representative paratypes. USA, California: Lassen Co., burnt area near Hallelujah Junction, west of Hwy 395 and south of Hwy 70, elevation 4900 ft. (1493 m), Williams 74-L-36 (CAS 637594! 637696! RENO 24591!). Nevada: Washoe Co, Rancho San Rafael, NW Reno, near Evans Creek, north of McCarran, dry hillside, Williams 85-295-2 & A. Tiehm. (RENO 24398! 68666!). Oregon: Lake Co., dry field, Lakeview, elevation 4802 ft. (1464 m), M. E. Peck 15489 (DS 171540! WTU 20545!). Lake Co., Paisley, elevation 4369 ft. (1332 m.), J. S. S. Elder 1915 (OSU 3596!).

Description. Erect to decumbent, smallish plant, branched from base, 3–4 dm tall. Branches all ending around the same height at maturity. Leaf blades narrowly elliptic, rarely lobed, few ca. 1.5 (2) cm long x \leq 0.7 cm wide, base slightly cuneate to obtuse, apex narrowly round. Upper leaves narrowly elliptic, but slightly smaller, entire. Inflorescences narrow paniculate spikes, flowers ca. 1 mm in diameter. Fruits ca. 1.2 mm in diameter x ca. 0.6 mm thick, lenticular, but convex below, with equatorial margin round. Pericarp adherent, brown with diagnostic, protruding whitish to creamy spots.

English diagnosis. *Chenopodium howellii* is a smallish plant uniformly branched from base with a fairly northwestern distribution, unlike any other in this group. Further collections along the northern California border and adjacent states will help to establish those limits. Similar to *C. aureum* in that its secondary leaf blades are narrowly elliptic, it is a much more profusely branching plant, with most of its branches getting to approximately the same height. The pericarp is to a degree similar in color to *C. incognitum*, but *C. howellii* it is smaller more compact plant and of very different appearance to *C. incognitum*.

Distribution & habitat. California: Alpine, El Dorado, Lassen, Modoc, Mono, Plumas, Siskiyou, and Tulare counties. Nevada: Washoe & Carson City counties. Oregon: Lakeview Co.

Phenology. *Chenopodium howellii* appears to flower in late June, and is in fruit from August to early September.

Etymology. Named in honor of botanist and taxonomist John Thomas Howell (1903—1994), founder of the RSA herbarium, curator of CAS herbarium.

Suggested common name. Howell's goosefoot

Chenopodium lineatum Benet-Pierce, sp. nov. (Fig. 3, center row). —TYPE: USA, California, Mono Co., Glass Mountain Region, Taylor Canyon Spring, perennial spring in narrow canyon running S-N, pumice soil with rhyolite outcrops above, open *Pinus jeffreyi* woodland with grazed *Artemisia tridentata*/*Purshia tridentata* scrub, with *Populus tremuloides*, *Mimulus guttatus* DC., *Aquilegia formosa* Fisch. ex. DC., and others, occasional on road edges by stream, elevation 7400 ft. (2256 m), M. Honer 1476, 25 August 2001 (Holotype: NY 801483! Isotype: RSA 680706!).

Representative paratypes. California: Alpine Co., Hope Valley Wilderness Reserve, elevation 7300 ft. (2225 m), Benet-Pierce 400 with J.P. Pierce (SDSU 22002!). El Dorado Co., Echo summit on road to Placerville, elevation 7382ft (2250m), John Thomas Howell 15297 (CAS 271772!). Inyo Co., Pinyon belt, Sage Flat to Olancha Pass, elevation 7000 ft. (2134 m), John Thomas Howell 26662 (CAS 361702!). Inyo Co., Pinyon belt, Sage Flat to Olancha Pass, elevation 7000 ft. (2134 m), John Thomas Howell 26663 (CAS 361926! left plant only). Mono Co., north shore of Convict Lake between northeastern and western ends of the lake, elevation 7600 ft. (2316 m), G. D. Barbe 3435, with J.T. Howell & T.C. Fuller (CDA 0014803!).

Description. Erect small to medium size sparse plant, gray green, branched, 5–7 dm high. Leaf blades lanceolate, few lobed, ca. 2 cm long x \leq 0.9 cm wide, base cuneate, apex obtuse or acute, entire.

Secondary leaf blades elliptic or narrowly elliptic, ca. 1–3 cm long x 0.4–1.6 cm wide, apex acute, base cuneate. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 25 cm long, flowers sessile, ca. 1 mm in diameter. Fruits ca. 1.2 mm in diameter x 0.6 mm thick, lenticular, somewhat flat above and below, with a strongly acute equatorial margin. Pericarp adherent, with alternating dark brown colored radii or lines perpendicular to the equatorial margin both above and below, brown and light cream to white, these very salient lines in the pericarp giving the name to this taxon.

English diagnosis. *Chenopodium lineatum* is probably the easiest plant to identify by its fruit, as its shape is unusually flat with most a uniformly and persistent marked pericarp of brown radii from the center to the mostly acute margin. Very abundant in Mono and Inyo counties, this species differs from the sympatric species *C. eastwoodiae* in that *Chenopodium lineatum* is a weaker smaller plant and has thinner leaves and its pericarp, appears always lined, not only at late maturity like *C. eastwoodiae*; it differs from *C. luteum* that has a very distinctive yellow pericarp.

Distribution & habitat. California: Alpine, El Dorado, Inyo, Mono, and Tulare counties. Nevada: Washoe Co.

Phenology. The species appears to flower in July, and is in fruit from August to early September.

Etymology. The fruit pericarp shows very distinct lines, like radii, that give it its name, *lineatum*.

Suggested common name. Mono goosefoot.

Chenopodium luteum Benet-Pierce, sp. nov. (Fig. 3, top row). —TYPE: USA, California, Fresno Co, Lower Tent Meadow, Copper Creek Trail, south fork of Kings River drainage, elevation 7600 ft. (2316 m), J. Peñalosa 2121, 16 August 1961 (Holotype: CAS 457912!).

Representative paratypes. California: Fresno Co., Laurel Creek, elevation 9000 ft. (2743 m) P. H. Raven 6160 (note by Wahl about deserving separate recognition), (CAS 390823!). Fresno Co., Simpson Meadow, Middle Fork of Kings River, elevation 6000 ft. (2438 m), J. T. Howell 33781 (CAS 457875! TEX Howell 33781!). Fresno Co., Mono Hot Springs, elevation 6500 ft. (1981 m), P. H. Raven 6137 (note by Wahl about deserving separate recognition) (CAS 390821!). Inyo Co., Sierra Nevada, Independence Creek Canyon, gravelly roadside, Onion Valley Road, elevation 8000 ft. (2439 m), M. DeDecker 3350 (CAS 637595! RSA 624714!). Mono Co., Glass Mountain region, along FS Rd 3S01 (paralleling power line – E of Deer Springs), approximately 1000 m W of Benton Crossing Rd., 200 m west of cattle tank, gently east sloping outwash alluvium of dry canyon, soil mixed decom-

posed granite and pumice gravel, with *Purshia tridentata* (Pursh) DC., *Artemisia tridentata*, *Ephedra viridis* Coville, and occ. *Pinus monophylla* Torr. & Frém, area evidently grazed, common in road edges and in scrub, elevation 7120 ft. (2170 m) (UC 1787084! RSA 697299!). Mono Co., eastern Sierra Nevada mountains, Convict Creek, UC Sierra Nevada Aquatic Research Lab, Mt Morrison Rd, 0.8 mi NW of intersections with Hwy 395, annual, common along the entrance road and in open site in sagebrush scrub, with *Eriogonum baileyi* S.Watson, *Gayophytum diffusum* Torr. & A.Gray, elevation 7070 ft. (2155 m), A. Howald 2632 (UCR 224279!).

Description. Erect medium size plant, simple or branched, 2–9 dm high, dark green. Leaf blades trullate very occasionally unlobed, ca. 2.8 cm long x ca. 1 cm wide, base cuneate to obtuse, apex narrowly obtuse or acute. Upper blades lanceolate, elliptic, or narrowly elliptic, ca. 1–1.6 cm long x 0.9 to 0.6 cm wide, entire. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 25 cm long; flowers sessile, ca. 1 mm in diameter. Fruits ca. 1.2 mm in diameter, oblate to conical, ca. 0.7 mm thick; pericarp weakly adherent, frequently semi-adherent, from solid pale yellow to aging darker yellow.

English diagnosis. *Chenopodium luteum* appears to be common in two forms, either simple one-stemmed or multi-stemmed, both with lobed primary leaves and a characteristic fruit shape from oblate to occasionally conical with uniformly yellow pericarp. Further collections in Fresno County should help to determine if there are two varieties here. In primary leaf shape, *C. luteum* is reminiscent of some plants of *C. aureum*, but stems of the former are not reddish or weak, being a stronger plant overall with a very distinct fruit, particularly in its yellow pericarp and oblate to conical shape.

Distribution & habitat. California: El Dorado, Fresno, Inyo, Lassen, Mono, and Tulare counties.

Phenology. The species appears to flower in July, and is in fruit from August to early September.

Etymology. Latin *luteum*, meaning yellow. The pericarp of this taxon appears yellow.

Suggested common name. Yellow goosefoot.

***Chenopodium sandersii* Benet-Pierce, sp. nov. (Fig. 3, bottom row).** —TYPE: USA, California, San Bernardino Co., Cleghorn Canyon, occasional, roadsides and open sandy areas (e.g., drainage ways) in chaparral and oak shrub lands, elevation 4600 ft. (1402 m), Scott White 1852 with C. McGaugh & K. Beaman, 10 September 1993 (Holotype: UCR 100144!).

Representative paratypes. California: Riverside Co., San Jacinto Mountains, Idyllwild, S.E. part of town near Saunders Meadow, west end of Tahquitz View Dr, toward Crestview Dr. Rural residential

area with houses on large lots, vacant lots and remnant dry yellow pine forest with *Pinus coulteri* D.Don, *Pinus lambertiana* Douglas, *P. jeffreyi*, *Quercus wislizeni* A. DC., *Q. kelloggii* Newb., *Q. chrysolepis* Liebm., *Arctostaphylos pringlei* Parry, *Ceanothus leucodermis* Greene, and others, scarce erect annual on road edge, elevation 5600 ft. (1707 m), A. C. Sanders 40837 (UCR 242672!). San Bernardino Co., San Bernardino Mountains, along a dirt road just SW of the Cottonwood Guard Station, slopes W. of Silverwood Lake, thinned chaparral (fire break), with *Quercus wislizeni*, elevation 3600 ft. (1100 m), A. C. Sanders 15194 (UCR 113577!). San Bernardino Co., San Bernardino Mountains, Cleghorn Ridge, along FS road 2N 47 between FS road 3N22 and Hwy 138 near Silverwood Lake, steep sided granitic ridge with chaparral and lower margins of yellow pine forest, elevation 4500 ft. (1372 m), A. C. Sanders 14765 (UCR 81809!). San Bernardino Co., San Bernardino Mountains, dry chaparral and oak covered slopes S of Silverwood Lake, along FSR 2N59 ca. 2 miles E. of Cottonwood station, W of FSR 2N43 from Cedar Pines Park, under power lines, decomposed granite soil, an uncommon annual on the road shoulder 0.4 m. W of 2N43, elevation 3700 ft. (1150 m), A. C. Sanders 14964 (RSA 628598!; UCR 83371!). San Bernardino Co., San Gabriel Mountains, mouth of Shade Canyon, north fork Lytle Creek, silt loam flat in the sun, elevation 3419 ft. (1042 m), Louis C. Wheeler 10731 (BRIT Wheeler 10731! RSA 602945!).

Description. Large and erect plant, branched or occasionally one stemmed, ca. 5–7 dm tall, yellowish green. Leaf blades lance-ovate ca. 2–3.5 cm long x 1–1.2(1.5) cm wide, very rarely with basal lobes, base cuneate and apex obtuse or acute, entire. Upper blades elliptic, ca. 1–2 cm long x 0.7 cm wide, base cuneate, apex acute. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 45 cm long, flowers sessile, ca. 1 mm in diameter. Fruits conical below, with flatish cone tip, or occ lenticular ca. 1 mm in diameter x ca. 0.6 mm thick, with acute equatorial margin. Pericarp semi-adherent, weak, often lost below at the center of the cone or completely, with dark yellow to brown faint color lines.

English diagnosis. *Chenopodium sandersii* is a large plant, similar to some large specimens of *C. incognitum*, but only when the primary leaves are present. Otherwise, secondary leaves are very long lance-ovate in *C. sandersii* and broadly elliptic in most *C. incognitum*. The fruit of *Chenopodium sandersii* is also very characteristic, being small, conical, with a semi-adherent pericarp, and not larger oblate and with a strongly adherent brown and golden to reddish pericarp as *C. incognitum*.

Distribution & habitat. California: Los Angeles, Riverside, and San Bernardino counties.

Phenology. The species appears to flower in late June, and is in fruit from August to early September.

Etymology. Named in honor of Andrew Sanders (1953–), southern California botanist, curator of the UCR herbarium, and prolific collector of *Chenopodium*.

Suggested common name. Sander's goosefoot.

Chenopodium simpsonii Benet-Pierce, sp. nov.* (Fig. 4, top). —TYPE: USA, California, San Bernardino Co., San Bernardino Mountains, Mill Creek Canyon, FSR 1N12 (toward Morton Peak and Warm Spring Canyon), 0.1–0.25 m above Mill Creek Rd., moist roadside seep in chaparral on mountains slopes, annual, scarce on roadside, elevation 3300 ft. (1006 m), *A. C. Sanders 14159*, 12 July 2008 (Holotype: UCR 132956!).

Representative paratypes. California: Los Angeles Co., San Gabriel Mountains, Kratka ridge, elevation 7001 ft. (2134 m), *Sharon Dougherty s.n.*, 7 September 2001 (UCR 176994!). San Bernardino Co., San Bernardino Mountains, Cleghorn Canyon, elevation 4400 ft. (1341 m), *Scott D. White 1783A*. Los Angeles Co., Kratka Ridge, Los Angeles National Forest, Waterman Mtn., mixed conifer forest, elevation 6800 ft. (2073 m), *Sharon Dougherty s.n.*, 18 September 1997 (UCR 132651!). San Bernardino Co., San Bernardino Mountains, Cleghorn Canyon, elevation 4400 ft. (1341 m), *Scott D. White 1783B* (UCR 162964!). San Diego Co., Palomar Mountain, 500' south of the Palomar Mountain Volunteer Fire Department, 950' South East of the Canfield and East Grade Rd (S-7) intersection, mixed coniferous forest, burned October 2007, decomposed granite, south facing slope, *Suzann M. Leininger 274* (SD 257942!). San Diego Co., southwest of Combs peak canyon off Chihuahua/Lost Valley Rd, just northwest of Sky Oaks Field Station, on BLM lands, chaparral/oak woodland with *Adenostoma fasciculatum* Hook. & Arn., *A. sparsifolium* Torr., *Quercus agrifolia* var. *oxyadenia* (Torr.) J.T. Howell, *Q. ×acutidens* Torr., *Cercocarpus betuloides* Nutt., and *Lonicera subspicata* var. *denudata* Rehder, geology: mostly schist substrates, erect annual, rare, elevation 4610 ft. (1405 m), *Jon. P. Rebman 20327*, with J. Schlachter, L. Aerne Hains & volunteers (SD 209644!). San Diego Co., Cuyamaca Peak, elevation 6512 ft. (1986 m), *Frank F Gander 6508* (SD 22874!). San Diego Co., Pine Valley, elevation 3737 ft. (1139 m), *Frank F Gander 4465* (SD 18748!).

Description. Erect annual, ca. 7 dm high, branched, side branches weak. Leaf blades petiolate, narrowly lanceolate, entire ca. 2 cm long x ca. 1 cm wide, base cuneate and apex acute, rarely lobed. Upper blades narrowly elliptic, ca. 2 cm long x ca. 0.4 cm wide, apex and base acute. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 2.5 cm long, flowers sessile, ca. 1 mm in diameter. Fruits oblate to occasionally conical, ca. 1.2 mm in diameter x ca. 0.6 mm thick, with round or occasionally acute equatorial margin. Pericarp adherent, thick, brown with a pattern of alternating faint reddish or yellow lines, from the center to the margin, the lines becoming faint with age.

English diagnosis. *Chenopodium simpsonii* is the only species in this group to have narrowly lanceolate leaves that are rarely lobed. Some of the specimens that have been identified as *C. pratericola* have lanceolate leaves as well, but the pericarp is always non-adherent in these. We have very strong evidence that the adherence of the pericarp is of paramount taxonomic importance in *Chenopodium*.

Distribution & habitat. California: Los Angeles, Riverside, San Bernardino, and San Diego counties.

Phenology. The species appears to flower in late June, and is in fruit from August to early September.

Etymology. Named in honor of southern California botanist, taxonomist, and Professor of Botany at San Diego State University, Michael G Simpson (1953–).

Suggested common name. Simpson's goosefoot.

Chenopodium twisselmannii Benet-Pierce, sp. nov. (Fig. 4, center row). —TYPE: USA, California, Tulare Co., Kern Plateau, Monache Jeep Trail about 4 miles north of Blackrock Guard Station on way to Monache Meadows, elevation 8700 ft. (2652 m), *John Thomas Howell 43934*, with G. H. True, 20 September 1967 (Holotype: CAS 637604! Isotype: PAC 81227!).

Representative paratypes. California: Kern Co., Landers Meadow, disturbed soil near dwellings, sandy/gravelly, *Allium* sp., *Eriastrum* sp., *Eriogonum* sp., *Phacelia* sp., *Pinus sabiniana* D. Don, *P. monophylla*, elevation 6754 ft. (2059 m) *Benet-Pierce 465* with J. P. Pierce (SDSU 20536!). Kern Co. Kern Plateau, on road to Bartolas Country, east of Little Canell Meadow, elevation 7200 ft. (2195 m), *John Thomas Howell 41850* with G. H. True (CAS 637689!, 593843!), the latter of which Wahl noted on the specimen as perhaps an undescribed var.; PAC 81033!). Kern Co., Kern Plateau, southwest end of Big Meadow just east of Cherry Hill Road; elevation 7800 ft (2377 m), *John Thomas Howell 47177* with G. H. True (CAS 637602!). Tulare Co., Kern Plateau, Monache Jeep Trail about 4 miles north of Blackrock Guard Station on way to Monache Meadows,

* At the insistence of the first author and against the reservations of the second, *Chenopodium simpsonii* will bear its name in honor of Professor Michael G. Simpson as a tribute and great personal appreciation for his excellence in scientific and human mentorship, his unwavering encouragement, and his support both academic and institutional for the first author, without which this and recent contributions to the advancement of *Chenopodium* taxonomy would not have been possible.

elevation 8700 ft. (2652 m), *John Thomas Howell* 43933 with G. H. True (CAS 637603! PAC 81229!). Tulare Co., Kern Plateau, Monache Jeep Trail about 3.8 miles north of Blackrock Guard Station, small rather dense colony growing in disturbed loamy decomposed granite in a forest opening along a broad ridgeline, red fir forest, elevation 8800 ft. (2682 m), *Ernest C. Twisselmann* 13760 (CAS 593832! 637620!; USDA Kernville Twisselmann 13760!). Tulare Co., Kern Plateau, Piute Mountains, Brown meadow, plant well branched from the base, rather bushy, leaves dark green, growing in sandy soil under ponderosa pines, rare, elevation 7550 ft. (2301 m), *E. C. Twisselmann* 3192 (CAS 406154! 593823!). Tulare Co., Kern Plateau, summit of Bald Mountain, common in disturbed metamorphic rock and gravel, at the base of the lookout tower, open summit above Jeffrey pine forest, elevation 9430 ft. (2874 m), *E. C. Twisselmann* 16006 (CAS 593827! 637618! G 61435!). Tulare Co., Kern Plateau, North Meadow jeep road on the west side of Sherman Peak, scattered colony growing in loam, along a little-used primitive road, Jeffrey pine forest, elevation 8600 ft. (2621 m), *E. C. Twisselmann* 14669 with E. McMillan (CAS 593880!).

Description. Erect, large annual, branched from base, ca. 11 dm tall. Leaf blades petiolate, narrowly lance-ovate, mostly unlobed, ca. 2.5 cm long x ca. 1 cm wide, base cuneate to obtuse and apex obtuse, entire. Secondary leaf blades narrowly oblong, ca. 3–2 cm long x ca. 0.7 cm wide, apex and base obtuse to acute. Inflorescences terminal and axillary panicles of glomerate spikes, ca. 60–40 cm long, flowers sessile, ca. 1 mm in diameter. Fruits conical, ca. 1.2 mm in diameter x ca. 0.7 mm thick, with marked equatorial margin. Pericarp adherent, orange brown to golden yellow from the center of the abaxial cone to the margin, brown half way as it ages.

English diagnosis. *Chenopodium twisselmannii* is similar to *C. incognitum* in that it is large plant with mostly unlobed leaves, but differs in that its leaves are narrowly lanceolate and mostly unlobed and its fruit is conical. It differs from *C. wahlii* in its conical fruit and much taller height and from *C. brandegeae*, which is similar in size, by its larger and conical fruit and more profuse vegetative habit.

Distribution & habitat. California: High meadows in Fresno, Inyo, Kern, and Tulare counties.

Phenology. The species appears to flower in late June, and is in fruit from August to early September.

Etymology. Named in honor of botanist and cattle rancher Ernest Christian Twisselmann (1917–1972), authority on southern San Joaquin Valley flora and author of The Flora of Kern County.

Suggested common name. Twisselmann's goosefoot or High Meadow goosefoot.

Chenopodium wahlii Benet-Pierce, sp. nov. (Fig. 4, bottom). —TYPE: USA, California, San

Bernardino Co., San Bernardino Mountains, dry road shoulders north of Lake Arrowhead, elevation 5000 ft. (1524 m), *Peter H. Raven* 16726, 17 September 1961 (Holotype: CAS 438720! Isotypes: SD 53090! RSA 155844! GH Raven 16726! UC 234690!).

Representative paratypes. California: Los Angeles Co., San Gabriel Mountains, north of Prairie Fork, 1/4 mile SE of Blue Ridge Lookout, loose unstabilized soil from mica schist, south slope of the ridge, Elevation 8400 ft. (2560 m), *Louis C. Wheeler* 6320 (SD 230206! RSA 608296! TX Wheeler 6320!). Riverside Co., San Jacinto Mountains, head of the west fork of Snow Creek, with *Eriogonum* sp., elevation 7800 ft. (2377 m), *Louis C. Wheeler* 6138 (RSA 597521! OBI 70667! BRY 392764! BM Wheeler 6138!). Riverside Co., San Jacinto Mountains on loose roadside soil, 1-mile n. of Idyllwild, elevation 5500 ft. (1676 m), *H. E. Wahl* 21803 (SD 82781!). San Bernardino Co., San Bernardino Mountains, Pacific Crest Trail from Mission Springs to Onyx Summit, Jeffrey pine forest with *Abies concolor* (Gordon & Glend.) Lindl. ex. Hildebr., *Arctostaphylos patula* Greene and others on decomposed granite soil with boulders on mountain slopes, ca. 1 mile W of Coon Creek jumpoff, N slope of peak, elevation 8588 ft. (2561 m), *A. C. Sanders* 19508 with White & L. Lubinsky (UCR 94176!). San Diego Co., Cleveland National Forest, 6 miles NW of Mount Laguna Post Office via Sunrise Hwy, at the edge of access road to Pioneer Mail Picnic area off S-1, elevation 5250 ft. (1610 m), *Jerilyn Hirshberg* 2527 (SD 325121!). San Diego Co., roadside and clearing, Laguna Mountains, 6 miles sw of Mount Laguna, elevation 5738 ft. (1749 m), *Herbert A. Wahl* 21810 (GH Wahl 21810! NY 3336125! RSA 229874!). San Diego Co., Pine Valley, Palomar Mountain, elevation 3737 ft. (1140 m), *Frank F. Gander* 6204 (SD 22067!).

Description. Erect annual, branched, 4–8 dm tall. Leaf blades petiolate, narrowly elliptic, rarely lobed, ca. 2.8 cm long x ca. 0.9–1.5 cm wide, base cuneate, round, to obtuse and apex obtuse, round, or widely acute, entire. Upper blades narrowly elliptic, elliptic, to lanceolate, ca. 1.6 cm long x 0.6 cm wide, apex and base widely acute or round. Inflorescences terminal and axillary panicles of glomerate spikes ca. 40 cm long, flowers sessile, ca. 1 mm in diameter. Fruits slightly conical below, \leq 1.1 mm in diameter x 0.5 mm thick, with acute equatorial margins. Pericarp adherent brown to occasionally with random yellow spots, turning all brown with age.

English diagnosis. *Chenopodium wahlii* is similar to *C. twisselmannii* in its narrowly elliptic leaf blades, but *C. wahlii* is a much smaller and thinner plant with a very distinct fruit. It differs from the geographically nearby taxa, *C. incognitum* and *C. sandersii*, in the shorter, narrowly elliptic leaves and fruit with a thin brown pericarp. It differs as well from *C. brande-*

geae, which is a larger plant with a very distinct black and brown fruit pericarp.

Distribution & habitat. California: Los Angeles, Riverside, San Bernardino, San Diego, and Tulare counties.

Phenology. The species appears to flower in late June, and is in fruit from in September and October.

Etymology. Named in honor of H. A. Wahl (1900–1975), botanist, taxonomist, and faculty member at Pennsylvania State University for over 40 yr. Scientific authority on the taxonomy of the genus *Chenopodium*.

Suggested common name. Wahl's goosefoot.

CONCLUSIONS

Based on the clear correspondence between fruit and vegetative morphology (Benet-Pierce and Simpson 2014, 2017), we have presented a partial taxonomic treatment of western North American *Chenopodium* in this possibly artificial “narrow-leaved group”. We determined these taxonomic entities first from characterization of fruit morphology, followed by correlation with vegetative features of the species.

We have employed more than 550 specimens, constituting a very high percentage of all specimens of this group collected in California and other western North American states, and we have provided as detailed descriptions as possible from the specimens at hand.

As a result of these studies, we have reached important conclusions in going forward with the taxonomy of *Chenopodium*. First, most *Chenopodium* taxa are clearly diagnosed by details of their fruit and seed morphology. Fruits are at present the most definite basis for identification, as they are more constant than vegetative characters. The majority of specimens cannot be identified adequately without fruit or seed until taxa have been extensively studied and described in detail. Even then, fruits appear to be needed as confirmation due to the well-documented vegetative plasticity in the genus. Second, most *Chenopodium* plants are not as variable as assumed in the past. Each taxon has a distinctive vegetative aspect that can be readily appreciated once classified into viable taxonomic units based on fruit morphology. Even if the vegetative characters alone cannot definitively identify taxa now, the use of fruits will allow for greatly improved and more detailed descriptions, permitting vegetative characters to be more reliably correlated, perhaps especially as additional collections are obtained in the future. Third, *Chenopodium* is much more speciose than previously thought. While some taxa are constrained to small and localized areas, others are much more widespread. This paper covers but just a fraction of what we believe is the as yet un-described *Chenopodium* diversity present in North America. More taxa

are likely to be added now that fruit and seed features have been firmly established as stable and diagnostic complementing vegetative features. Of course, the taxonomy of *Chenopodium* will be further strengthened by molecular phylogenetic studies.

Finally, we note that early treatments of *Chenopodium* taxonomy in North America were incomplete. But we hope that with both stable and diagnostic fruit features, the task of studying, describing, and engaging in more encompassing treatments of this genus can become less subjective and, hopefully, a less frustrating undertaking. *Chenopodium* will greatly benefit by additional, extensive taxonomic work focusing on fruit and seed morphology in every region of the country, if not the world, where plants of this important, but misunderstood genus are still present. It is our wish that with improved identifications and descriptions, *Chenopodium* will also be better understood and appreciated for future protection and conservation.

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APPENDIX 1

KEY TO THE *CHENOPODIUM* SPECIES OF CALIFORNIA

MODIFIED FROM CLEMANTS AND BENET-PIERCE (2012)

1. Primary leaf blades generally 2-lobed or entire
 2. Primary leaf blade length generally $<1.7 \times$ width, most leaves deltate, triangular, ovate-oblong, or widely ovate
 3. Pericarp adherent to seed
 4. Plant scented, most primary leaf blades ovate-oblong to widely ovate; fruit > 1 mm not horizontally depressed; scarce, mostly Central Valley *C. vulvaria*
 - 4'. Plant not scented, most primary leaf blades deltate or occ ovate-oblong; fruit horizontally depressed on one side, <0.8 mm; relatively common NV & eastern CA *C. nevadense*
 - 3'. Pericarp free from seed
 5. Most primary leaf blades deltate, triangular, or elliptic with prominent basal lobes; seed black
 6. Plant erect, reddish in age, few-branched distally; seed in side view lenticular, margin thick, square *C. fremontii*
 - 6'. Plant compact, rounded, dull green in age, many-branched distally; seed in side view rhomboidal, margin obtuse. *C. incanum* var. *occidentale*
 - 5'. Most primary leaf blades ovate-oblong to elliptic and only some primary leaf blades with basal lobes; seed coat generally reddish-brown *C. atrovirens*

2'. Primary leaf blade length generally $>1.7 \times$ width, most leaf blades linear, narrowly lanceolate to widely ovate, oblance-ovate, narrowly to broadly elliptic, or trullate

7. Primary leaf blade length generally 4-many \times width, linear, narrowly lanceolate, lanceolate to lance-ovate

8. Pericarp adherent to seed; plant generally branched from base; primary leaf blade linear or narrowly lanceolate;

9. Primary leaf blade linear, generally <3 mm wide; fruit ≤ 0.7 mm . . . *C. leptophyllum* aggregate

9'. Primary leaf blade narrowly lanceolate, generally ≥ 3.5 mm wide, fruit ~ 1 mm; S. CA *C. simpsonii*

8'. Pericarp free from seed; plant with long acaulescent stem, primary leaf blade lance-ovate *C. pratericola* aggregate

7'. Primary leaf blade length 1.7–4 \times width, narrowly elliptic to broadly elliptic, narrowly lanceolate to lanceolate, trullate to widely trullate, widely lance-ovate to widely ovate, or oblance-ovate

10. Pericarp free from seed; plant prostrate or nearly so

11. Stems procumbent; primary leaf blade trullate; seed lenticular in side view, seed coat rugose, not shiny; coastal sand dune habitat *C. littoreum*

11'. Stems decumbent; primary leaf blade narrowly elliptic; seed flat in side view, seed coat tessellate and very shiny; sage brush habitat. *C. nitens*

10'. Pericarp adherent to seed; plant erect

12. Plant regularly ≤ 5 dm

13. Plant weakly branched, stems reddish at different height levels at maturity; primary leaf trullate and lobed; pericarp golden & shiny *C. aureum*

13'. Plant many branched from base, stems not red, usu all ending at same height at maturity, primary leaf blade narrowly elliptic, rarely lobed; pericarp brown or black color with white protuberances *C. howellii*

12'. Plant regularly ≥ 5 dm;

14. Primary leaf blades unlobed or occ lobed, narrowly elliptic, lanceolate or narrowly lance-ovate

15. Primary leaf blades occasionally lobed, narrowly elliptic, narrowly lanceolate to broadly lanceolate

16. Plant usually 5–8 dm, leaf blades gen narrowly elliptic or broadly lanceolate; fruit lenticular in side view

17. Plant many branched from base; leaf blades narrowly elliptic to broadly lanceolate; fruit equatorial margin obtuse, pericarp usu brownish; So CA *C. wahlii*

17'. Plant thinly branched; leaf blades broadly lanceolate to lanceolate; fruit equatorial margin acute; pericarp with brown radii from the center to the margin; El Dorado, Mono, Inyo and Tulare counties *C. lineatum*

16'. Plant usually to 11 dm, leaf blades narrowly lance-ovate; fruit conical in side view; high meadows, Fresno, Kern & Tulare Co. *C. twisselmannii*

15'. Primary leaf blades unlobed, elliptic or lance-ovate

18. Plant simple or branched; primary leaf blades lance-ovate; secondary leaf blades elliptic; fruit distally conical in side view, margin acute, pericarp golden brown; so. CA *C. sandersii*

18'. Plant thinly branched; primary leaf blades elliptic or lance-ovate; secondary leaf blades occ falcate; fruit lenticular in side view, pericarp black and gold markings, very shiny; San Diego Co. *C. brandegeae*

14'. Primary leaf blades usually lobed, trullate, broadly elliptic or broadly lance-ovate

19. Plant usually ≥ 8 dm; fruit lenticular or oblate; pericarp golden or reddish brown or cream

20. Primary leaf blades broadly lance-ovate; fruit oblate in side view, margin rounded, >1.4 mm in diameter in side view, pericarp thick, striped either brown, cream, or reddish in color; El Dorado, Mono and Tulare counties *C. eastwoodiae*

20'. Primary leaf blades broadly elliptic or trullate; fruit lenticular in side view, margin acute, ~ 1.2 mm in diameter; pericarp golden-brown or reddish brown with cream color papillae markings; widespread in western North America *C. incognitum*

19'. Plant usually ≤ 8 dm; fruit wide-oblate, pericarp yellow; El Dorado, Fresno, Inyo, Lassen, Mono counties. *C. luteum*

1'. Primary leaf blades 2-lobed and toothed

21. Pericarp adherent

22. Pericarp light gold color, honey-combed pitted at 20x magnification *C. berlandieri*

23. Style base not yellow in fruit; seed 1–1.3 mm diam. var. *simuatum*

23'. Style base yellow in fruit; seed 1.2–1.5 mm diam var. *zschackei*
 22'. Pericarp brown, papillate at 20 \times *C. strictum* aggregate
 21'. Pericarp free from the seed
 24. Plant to 1 m; inflorescence branches straight; flower clusters generally in axillary and terminal branched panicles *C. album* aggregate
 24'. Plant to 2 m; inflorescence branches \pm curved or pendent; flower clusters in axillary and terminal panicles of spikes *C. missouriense*

APPENDIX 2

CHENOPODIUM TAXONOMIC KEY BASED ON FRUIT CHARACTERS FOR TAXA IN THIS PAPER

1. Fruit conical or slightly conical below
 2. Fruit conical below, golden-brown or reddish-brown
 3. Pericarp golden-brown
 4. Fruit \leq 1 mm pericarp semi-adherent *C. sandersii*
 - 4'. Fruit \sim 1.2 mm pericarp adherent *C. twisselmannii*
 - 3'. Pericarp reddish-brown with scattered white papillae *C. hians*
 - 2'. Fruit slightly conical below, pericarp uniformly brown in color. *C. wahlii*
 - 1'. Fruit lenticular or oblate
 5. Fruit lenticular in shape
 6. Fruit convex on both sides, pericarp very shiny
 7. Pericarp golden. *C. aureum*
 - 7'. Pericarp brown and black colored *C. brandegeae*
 - 6'. Fruit convex or flat below, pericarp dull
 8. Fruits convex below, flat above; pericarp with white protuberances or lines *C. howellii*
 - 8'. Fruits flat below and above; pericarp with brown radii. *C. lineatum*
 - 5'. Fruit oblate in shape
 9. Pericarp thick
 10. Fruit diameter \geq 1.4 mm, pericarp striped in age. *C. eastwoodiae*
 - 10'. Fruit diameter \leq 1 mm, pericarp striped early. *C. simpsonii*
 - 9'. Pericarp thin
 11. Fruit \sim 1mm pericarp semi-adherent, yellow *C. luteum*
 - 11'. Fruit \geq 1.2 mm pericarp strongly adherent, golden and brown *C. incognitum*

CLARIFICATION OF THE NAME *CYLINDROPUNTIA WOLFII* (CACTACEAE) AND AN ACCOUNT OF THE SPECIES

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ABSTRACT

The name *Cylindropuntia wolfii*, which has been used for a distinct cholla species, has had a problematic nomenclatural history. An attempt is made to clarify the validity of the name and to provide a revised description of the species and its presently-known distribution.

Keywords: Cactaceae, *Cylindropuntia wolfii*, description, distribution, nomenclature, typification, validation.

The name *Cylindropuntia wolfii* represents a distinct dioecious or subdioecious hexaploid endemic to southern California and extreme northern Baja California (Benson 1969; Pinkava et al. 1992; Baker et al. 2009, 2012; Rebman and Pinkava 2001; Baker and Pinkava 2018). Populations of the taxon were first described as *Opuntia echinocarpa* Engelmann & J.M. Bigelow var. *wolfei* L.D. Benson (Benson 1969). However, Benson's name was invalid because he did not designate a specimen from a single gathering as a holotype and instead combined two collections from separate dates as a "type" (see Art. 40.2, ex. 1, Turland et al. 2018).

Based on coloration of floral parts, morphology, and chromosome number, Baker in Pinkava et al. (1992) elevated the taxon to species level, "*Opuntia wolfii* (L.D.Benson) M.A.Baker", and corrected the orthography of the epithet. Although, this did not validate the original basionym because a holotype was not designated (See Art. 40.6, Turland et al. 2018), it inadvertently became the name of a new species, *O. wolfii* M.A.Baker, because it was associated with a full and direct reference to an earlier protologue and was assigned a single specimen from one gathering as the type. Instead of using the term "holotype" Baker used "lectotype" but this is considered an "error to be corrected" (See Art. 9.10, Turland et al. 2018).

It is the intent herein to clarify the nomenclatural history of the name *Cylindropuntia wolfii* and its authorship, and to provide a revised description and distribution for the species with more information than was available to Benson.

NOMENCLATURAL HISTORY

Opuntia echinocarpa var. *wolfei* L.D.Benson. Cact. Succ. J. (Los Angeles) 41: 33. 1969. Nom. inval. See ICBN Art. 8.2, ex. 3 (Turland et al. 2018).—Type: Base of Mountain Springs Grade, Imperial County, California, western edge of the Colorado Desert on U.S. 80 west of El Centro, *Carl B. Wolf* 9429, June 12, 1938, (RSA 20700!).

gation (RSA 96387), "the two sheets together the holotype" [the second sheet not found]. Isotypes: US box, 3052212!, UC592967!, CAS0214893!. Because the type was not designated from a single gathering, it is illegitimate. Benson also designated as "isotype" a collection by Balls (19004) made on "April 12, 1954" from the type individual growing in the RSA garden (UC043499! [not 1043499 per Benson], CAS402031!, RSA96337!). However, because the material was collected on a different date and not by Wolf himself, it is a separate gathering and thus a paratype.

Opuntia wolfii M.A.Baker. Madroño 39(2): 108. 1992, as *O. wolfii* (L.Benson) M.A.Baker.—Holotype ["Lectotype"]: Base of Mountain Springs Grade, Imperial County, California, western edge of the Colorado Desert on U.S. 80 west of El Centro, *Carl B. Wolf* 9429, June 12, 1938, (RSA 20700!); ISOTYPES: CAS 214893!, UC 592967! (Box), US 03052212! (Box).

Although ASU 155254 (photo) was designated as an isolectotype by Pinkava et al. (1992), this material was not available to the author of the original protologue and, therefore, cannot be chosen as a lectotype (Staples and Prado 2018).

Cylindropuntia wolfii (M.A.Baker) M.A.Baker. J. Arizona-Nevada Acad. Sci. 33: 150, 2001 (as *C. wolfii* (L.D. Benson) M.A.Baker). Although the basionym is listed as the invalid name *Opuntia echinocarpa* Engelmann & J.M. Bigelow var. *wolfei* L.D.Benson, there is a full and direct reference to *Opuntia wolfii* M.A.Baker ["*Opuntia wolfii* (L.D.Benson) M.A.Baker"].

REVISED DESCRIPTION

Densely-branched dioecious or subdioecious shrub to 1.5 m tall, the branches generally originating from the base and often strict; stem segments yellow-green to gray-green, up to 40 cm long and 4 cm in diameter; stem tubercles prominent to 1 cm broad and 1.5 (2) cm high, the upper ends tending to abruptly angle toward the stem, forming a shelf on

which lies the areole; areoles orbicular to obdeltate, to 7 mm at the widest, pubescence tan to yellow-brown, aging gray; spines to 30 per areole (often proliferating on older stems), pale brown to yellow-brown, aging dark brown, to 3 cm in length; spine sheaths mostly translucent yellow; glochids in an adaxial tuft and scattered along areole margin, yellow-brown to pale brown; inner tepals of flowers yellow-green, more often orange to dark purple-red, to 35 mm in length, stamen filaments magenta to dark purple-red, anthers yellow on staminate individuals, empty and pale on pollen-sterile individuals. Mature fruits dry, fertile fruits subspherical, to 30 mm long, sterile fruits narrow. Seeds generally occurring only in male-sterile individuals, tan, flattened, orbicular, to 6 mm dia. $2n = 66$ (determinations from seven individuals, including one collection from Baja California).

Flowering March through May. Sonoran Desert scrub, rocky slopes and hills; 300–1200 m; southwestern California, extreme northern Baja California (Fig. 1).

REPRESENTATIVE SPECIMENS

MEXICO, BAJA CALIFORNIA: 42 km W of Mexicali at km marker 42 on Hwy 2 between Tecate and Mexicali., 14 March 1992, Rebman & Cordova 1280 (ASU); bottom of La Rumorosa along MEX Rte 2 between Tecate and Mexicali., 17 April 1994, Rebman 2617 (ASU, BCMEX, HCIB); E slope of the Sierra de Juárez along Hwy 2, 25 April 1985, Sanders & Neisess 5728 (ASU, UCR); Sierra Juárez, 45km W of Mexicali, N side of Mexico Hwy, 9 March 2013, Baker & Cloud-Hughes 17695 (ASU). **USA, CALIFORNIA, Imperial County:** 12.5 mi N of Interstate 8, off Ogilby Road, 10.1 mi E on Hayduke Mine Road, 13 April 1994, Dietrich et al. 40 (MO); plateau above Mountain Springs, 10 June 1919, McGregor 887 (CAS); Mountain Springs Grade between Jacumba and Ocotillo: along I-8 at Mountain Springs Road, 19 March 1997, Rebman & Salywon 3820 (SD, UCR); 7.1 mi. NW of junction with I-8, 0.3 mi. S of San Diego County line., 19 March 1997, Rebman & Salywon 3823 (SD, UCR); Mountain Springs Grade near I-8 exit., 19 April 2000, Rebman et al. 6521 (DES, SD, UCR); 2 to 3 km S of Ocotillo on Hwy 98, just S of the intersection with I-8., 31 August 1986, Baker 7043 (ASU, DES); Mountain Springs Grade, just S of interstate 8, 04 May 2001, Rebman & Solis, 7306 (DES, RSA, UCR, SD, SDSU); Mountain Springs Grade, just S of Interstate 8., 04 May 2001, Rebman & Solis, 7307 (DES, RSA, UCR, SD), 7308 (BCMEX, DES, SD, SDSU, UCR); 1k SW of Sugarloaf Mountain., 13 April 1987, Baker & Parfitt 7533 (ASU, DES); 1 kw SW of Sugarloaf Mountain, 13 April 1987, Baker & Parfitt 7534 (ASU, DES); Mountain Springs Road and Freeway 8., 13 April 1987, Baker & Parfitt 7536 (ASU, DES); 1.5 k S of Ocotillo, 13 April 1987, Baker & Parfitt 7539 (ASU, DES); **Mountain Springs Grade; base, 12 June 1938,**

Wolf 9429 (CAS, RSA, UC, US); Canyon 1.7 mi S of Hwy. 78, 25 March 1957, Wiggins, 14090 (CAS); Rte. I-8 turnoff at Mountain Springs between two halves of freeway, 25 May 1984, Pinkava et al. 14301 (ASU); 30m E of the San Diego County line, 8.5km WSW of Carrizo Mountain, 14 December 2011, Baker & Cloud-Hughes 17481 (ASU); N edge of San Felipe Creek, 950m NNW of Harper's Well, 11 September 2012, Baker & Cloud-Hughes 17611 (ASU, RSA, SD); Jacumba Mountains, 500m E of Devils Canyon, 4km NNE of Mountain Spring, 25 May 2016, Baker & Chow 18574, 18575 (ASU); 6.9 mi NW from Ocotillo, 05 November 1957, Balls & Everett 22678 (UC); along dirt road 0.6 mi. W of Imperial Hwy (Hwy S2), 7.5 mi NW of town of Ocotillo, just E of San Diego County line, 03 March 2015, André 31321 (GMDRC, RSA); Coyote Wells, 01 April 1905, Brandegee s. n. (UC); **San Diego County:** near Boulder Park along hwy 80, 11 May 1950, Rush 119 (POM); Mortero Canyon Rd., 1/4 mi NE of intersection with S2, 27 March 2008, Hains et al. 145 (ASU, DES, SD); Jojoba wash jeep trail, 176 yards W of County Road S2, 12 March 2009, Sullivan 644 (ASU, SD); Jacumba, eastbound I-8, 1 mi NW of In-Ko-Pah exit, 12 May 2009, Sullivan 720 (DES, SD); 2 mi SE of Mortero Palms, at end of road to Syd Haden Spring, 19 March 2005, Gregory et al. 1354 (DES, SD); near I-5, 5 mi W of Jucumba, 02- May 1970, Gibson 1702 (RSA); E of S-2 near dirt road parallel to Carrizo Creek; 19 April 2011, Nenow 1781 (SD); Carrizo Canyon, at mouth of tributary canyon (Four Frogs Canyon) to the W of Carrizo Canyon, 23 March 2009, Hendrickson et al. 3440 (ASU, DES, SD); between Jacumba and Inkopah; N of I-8 and N of old Hwy 80, 22 May 1997, Rebman & Rea 4090 (SD); 3 km SE of Sweeney Pass, 17 March 1984, Baker 4917 (ASU); NW of Ocotillo, W side of Coyote Mountains, just east of Highway S2, near Mortero Wash, 22 March 1998, Rebman et al. 4935, (SD); Mortero Wash, 0.2 mi east of S2, 30 March 1998, Rebman 4978 (BCMEX, SD); near head of grade between Jacumba and Mountain Springs, 18 April 1928, Ferris 7058 (CAS); 5.3 km NW of San Diego-Imperial county line; ca. 4 km SE of Sweeney Pass, 13 April 1987, Baker & Parfitt 7532 (ASU, DES); S slope of canyon of San Felipe Creek, near foot of Sentenac Canyon, 20 April 1928, Peirson 7853 (RSA); near junction of Grapevine & San Felipe Creeks, Sentenac Valley, 25 April 1920, Jepson 8784 (JEPS); Lower Box Canyon, 29 April 1941, Gander 9280 (SD); W of Ocotillo; eastern base of Jacumba Mountains; vicinity of Mortero Palms, 19 March 2005, Rebman et al. 11336 (DES, SD); near Sentenac Canyon; Wagon Wash, 21 April 1928, Jepson 12501 (JEPS); .5km ESE of Sweeney Pass, 13 March 1998, Baker 12785 (ASU); Mountain Springs, near the San Diego Co. line, US 80., 13 July 1963, Benson 16372 (POM); 13 km NW of Ocotillo, 8.7 km WSW of the summit of Carrizo Mountain, 14 December 2011, Baker & Cloud-Hughes 17482 (ASU), 17483 (ASU, SD); Mountain Springs Grade, 6 mi ENE of Jacumba,

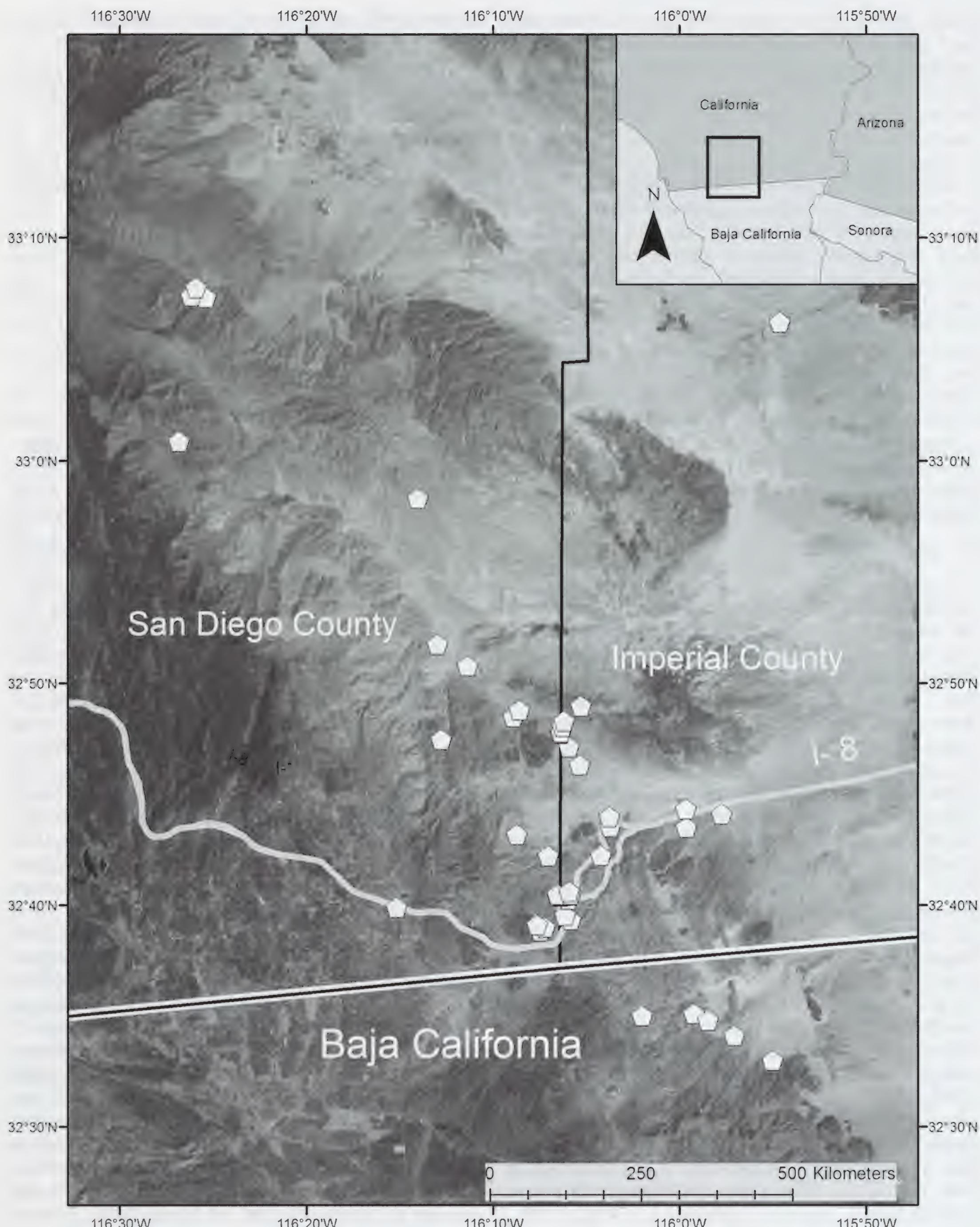


FIG. 1. Vouchered localities for *Cylindropuntia wolffii* (white pentagons).

W of Interstate 8, 24 April 2007, Ward et al. 26 (DES); Mountains Springs, 09 May 1894, E. Mearns [probably] s. n. (US); Rte. S-2, 2.7 mi NW of Imperial County Line, 25 May 1984, Pinkava et al. 4300 (ASU).

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SONCHUS TENERRIMUS (ASTERACEAE) IN NORTH AMERICA NORTH OF MEXICO

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ABSTRACT

Some reports of *Sonchus tenerrimus* L. for North America north of Mexico, notably from Alabama and California, are based on misidentified specimens of *S. oleraceus* L.

Key Words: *Sonchus*, *S. oleraceus*, *S. tenerrimus*.

In 2018, I came to file a specimen from Butte County, California, labeled *Sonchus tenerrimus* L. (JEPS127078, *L. Ahart* 20691). That specimen differs markedly from the 2 specimens in the UC folder for California specimens of *S. tenerrimus* and it does not match well any of the 38 specimens filed as *S. tenerrimus* in UC from Africa, Europe (+ Near East), and Mexico. The Butte Co. specimen does closely match some of the 159 specimens filed as *S. oleraceus* L. in JEPS and UC from Africa, Europe (+ Near East), and North America north of Mexico (including 92 from California). I was led to review reports of *S. tenerrimus* for North America north of Mexico. Here, I summarize my findings.

Alabama: C. Mohr (1901) reported *S. tenerrimus* from ballast sites. Based on pictures, I have identified two specimens from Alabama, both labeled *S. tenerrimus* and believed to be the basis of Mohr's reports, as belonging within the circumscription of *S. oleraceus*: UNA00049995, Mobile Co., Ballast ground, near mouth of Mobile river, *C. Mohr* s.n., September, 1885; UNA00050000, Mobile Co., Ballast, estuary Mobile river, *C. Mohr* s.n., July 4, 1893).

California: From specimens in UC and specimens in other herbaria, I note that *S. tenerrimus* L. was collected in or near San Diego, CA, by T. Nuttall in 1836 (specimens in BM, GH, K, PH), by C. R. Orcutt in 1884 (UC), by T. S. Brandegee in 1895 (NY), and by C. A. Purpus in 1898 (UC). Specimens of *S. tenerrimus* from the Channel Islands, CA, include San Clemente Island (*B. Trask* s.n., 1903, NY), San Nicolas Island (*B. Trask* s.n., 1900–1904, NY, RSA), Santa Barbara Island (*R. N. Philbrick* B68-82, 1968, SBBG; *R. N. Philbrick*, *J. K. McPherson* B68-247, B68-249, SBBG; *R. N. Philbrick* B69-111, 1969, SBBG), and Santa Catalina Island (*B. Trask* s.n., 1901, NY).

From pictures of specimens provided by the individuals acknowledged below, I have identified as *Sonchus oleraceus* L. the following specimens cited in the Consortium of California Herbaria database (CCH) (Consortium of California Herbaria 2019) as *S. tenerrimus* L.: **Butte Co.**, 1974-06-03, *L. Ahart* 474, CHSC31658; 1982-10-11, *M. S. Taylor*, *L. Ahart* 5050, CHSC37529; 1984-11-01, *L. Ahart* 4832, CAS-

BOT-BC374754; 1996-05-27, *V. H. Oswald*, *L. Ahart* 7670, CHSC66157; 2015-11-01, *L. Ahart* 20691, CHSC116495; **Contra Costa Co.**, 1998-05-08, *G. F. Hrusa*, *D. Crowe* 14376, UCD146721(DAV205102); **Marin Co.**, 2002-08-01, *R. E. Preston* 1942, UCD78007(DAV156009); **San Diego Co.**, 1977-05-06, *D. F. Howe* 4937, SD113009; 1994-01-22, *J. W. Brown* MM85, SD138162; 2004-08-24, *J. Barth* 102, SD158778; 2008-05-24, *J. K. Snapp-Cook* et al. 140, SD205517; 2014-05-18, *R. L. Breisch* 1104, SD253037; **Santa Barbara Co.**, 1969-03-15, *R. N. Philbrick*, *D. W. Ricker* B 69-45, SBBG32816; **Santa Clara Co.**, 1931-10-11, *D. D. Keck* 1306, CAS-BOT-BC374755; 1971-11-17, *L. A. Olsen* 72, SJSU8163; **Santa Cruz Co.**, 1998-09-05, *R. Morgan* 3359, UCSC008244; **Sutter Co.**, 2008-04-17, *G. K. Helm-kamp*, *E. A. Helm-kamp* 13280, UCR198409; **Tulare Co.**, 1969-04-23, *J. Rockwell* 69-0513, CAS-BOT-BC374756; **Ventura Co.**, 1989-04-24, *S. A. Junak* SN365, SBBG106303; 1993-05-19, *S. A. Junak* SN1117, CAS-BOT-BC374757, SBBG106146.

Additional specimens of *S. oleraceus* from California, filed in herbaria as *S. tenerrimus* and not cited in CCH are: **Orange Co.**, 1980-07-11, *G. A. Marsh* s.n., IRVC17234; 1980-07-11, *G. A. Marsh* s.n., IRVC17923; 1985-03-12, *F. M. Roberts* and *G. A. Marsh* s.n., IRVC21943; **San Luis Obispo Co.**, 1986-05-01, *C. F. Smith* 12073, SBBG08381.

New Jersey: Specimens of *S. tenerrimus* from ballasts at Camden (*A. Pollard* s.n., September 22, 1897, NY), at Jersey City (*S. Brown* s.n., 1879, NY), and at Kaighn Point (*I. Burk* s.n., no year, PH).

New York: A specimen of *S. tenerrimus* from Staten Island (*A. Hollick*, s.n., September 20, 1908, NY).

Pennsylvania: A specimen of *S. tenerrimus* from ballast at Philadelphia (*Isaac Burk* s.n., September 19, 1879, NY).

Difficulties in distinguishing between *Sonchus oleraceus* and *S. tenerrimus* because of morphological similarities have been noted repeatedly. For example, to distinguish between the two species Boulus (1960) provided a couplet based solely on corolla traits: "Ligule and corolla-tube of equal

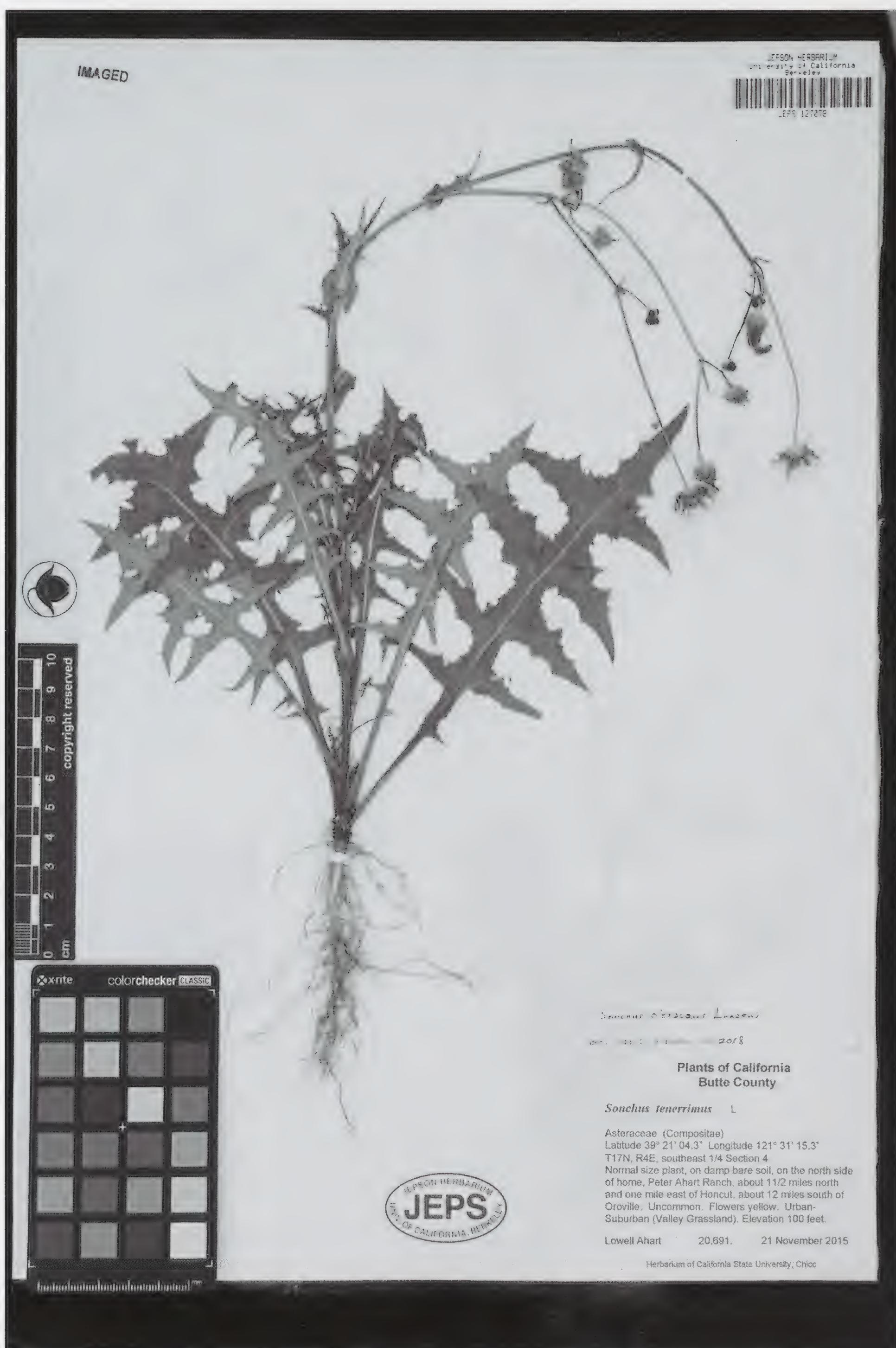
FIG. 1. *Sonchus oleraceus*, JEPS127078.



FIG. 2. *Sonchus tenerrimus*, UC1235769.

length... *S. oleraceus*; Ligule longer than corolla-tube... *S. tenerrimus*" (Pp. 412).

Regarding *S. oleraceus*, Jeanes (1999) wrote, "A very variable species that is often difficult to distinguish from *S. tenerrimus* with any confidence" (Pp. 697). Boulus (2002) wrote, "*Sonchus oleraceus* is a polymorphic species which grows in diverse habitats. Its variability might be due to its probable allopolyploid origin (2n=32), as a hybrid between *S. asper* (2n=18) and *S. tenerrimus* (2n=14)" (Pp. 311).

Based on pictures of lectotype specimens of *Sonchus oleraceus* L. and *S. tenerrimus* L. (JSTOR Global Plants 2019) and study of specimens in JEPS and UC, including those pictured in Figs. 1 and 2, I offer the following couplet:

1. Leaf blades: lobes mostly broadly deltate to narrowly triangular, ultimate margins usually coarsely dentate; corollas: tube \pm equal to ligule. *S. oleraceus*
- 1' Leaf blades: lobes mostly oblong to linear, ultimate margins entire or denticulate; corollas: tube shorter than ligule. . . *S. tenerrimus*

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